SOME STROPHOMENACEAN BRACHIOPODS FROM THE BRITISH LOWER SILURIAN

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CONTENTS

SYNOPSIS

The brachiopod family Leptaenidae is relegated to subfamilial rank within the Strophomenidae. All the known British Lower Silurian (Llandovery) species from the revised family Strophomenidae are described and figured. Two new genera are erected: *Katastrophomena*, type species *Strophomena antiquata* var. *woodlandensis* Reed 1917, and *Mackerrovia*, type species *Brachyprion arenaceus* var. *lobatus* Lamont & Gilbert 1945. Two new subgenera are erected within the genus *Cyphomena* Cooper 1956 (hitherto thought to be confined to the Ordovician): *Cyphomenoidea*, type species *Leptaena wisgoriensis* Lamont & Gilbert 1945, and *Laevicyphomena*, type species *C. (L.) feliciter* sp. nov. Eight new species and one subspecies are erected, and the ecological communities of all the species recorded.

I. INTRODUCTION

THREE families of the superfamily Strophomenacea occur in the British Lower Silurian. One, the Stropheodontidae, has already been considered (Cocks 1967), and thus the present paper is concerned exclusively with representatives of the other two families, the Strophomenidae and the Leptaenidae.

Strophomenids are widely distributed in the Lower Silurian of Britain, but are sporadic and rare at most localities. They have been recorded under the name '*Strophomena antiquata*' in most faunal lists. Leptaenids are rather commoner and have usually been referred to '*Leptaena rhomboidalis*'. Although the Wenlock species of both families have been figured for many years, notably by Thomas Davidson in various works, the Llandovery species have remained for the most part poorly described.

The stratigraphy and correlation of the British Llandovery is at the present time under review, and a joint paper by Dr. A. M. Ziegler, Dr. W. S. McKerrow and the present author is in course of preparation. Correlation between the various areas and the type area of Llandovery itself has been effected mainly by the use of evolving brachiopod lineages such as those of *Stricklandia* (Williams 1951) and *Eocoelia* (Ziegler 1966).

II. SYSTEMATIC DESCRIPTIONS

Superfamily **STROPHOMENACEA** King, 1846

Classification

In the recent Treatise (Williams *et al.* 1965), the classification of the Strophomenacea is as follows:

Superfamily Strophomenacea King 1846 (L.Ord.-L.Carb.)
- Family Strophomenidae King 1846 (L.Ord.-L.Dev.)
  - Subfamily Strophomeninae King 1846 (M.Ord.-U.Sil.)
  - Furcitellinae Williams 1965 (M.Ord.-L.Sil.)
  - Rafinesquininae Schuchert 1893 (M.-U.Ord.)
  - Glyptomeninae Williams 1965 (L.-M.Ord.)
  - Oepikinae Sokolskaya 1960 (M.-U.Ord.)
  - Leptaenoideinae Williams 1953 (U.Sil.-L.Dev.)
- Family Foliomenidae Williams 1965 (U.Ord.)
- Family Christianiidae Williams 1953 (Ord.)
- Family Leptaenidae Hall & Clarke 1894 (M.Ord.-L.Carb.)
- Family Stropheodontidae Caster 1939 (U.Ord.-U.Dev.)

The Stropheodontidae is divided into seven subfamilies which are outside the scope of the present paper; the family is distinct in possessing denticles, and was held with some justification to possess superfamilial status by Sokolskaya (1960 : 213). Of the remaining families, the Foliomenidae and the Christianiidae are confined to the Ordovician, leaving the Strophomenidae and Leptaenidae to be considered here.

There is some doubt as to whether these two families are validly separable. Apart from the undiscussed list at the end of Hall & Clarke (1894 : 353–354), which divided what are now known as the suborders Strophomenidina and Triplesiidina into a rather arbitrary division between Strophomenidinae and Leptaenidae (thus creating the latter family), the two families were not divided again until 1956 in Cooper's great work on the Chazyan brachiopods. Thus Williams in his paper on strophomenoid classification (1953) did not mention the Leptaenidae: he divided the Strophomenacea into three families, the Strophomenidae, Stropheodontidae and Christianiidae, and the Strophomenidae was divided into only two subfamilies, the Strophomeninae and the Leptaenoideinae. In fact he specifically cited the Rafinesquinidae and Strophomenidae as synonymous (1953 : 8).

Cooper (1956) divided the Chazyan Strophomenacea into three families, Leptaenidae, Christianiidae and Strophomenidae. He briefly defined the three families as follows—Leptaenidae: ' Compressed to faintly lenticular Strophomenacea with large apical foramen ' (1956 : 820); Christianiidae: ' Smooth or finely costellate Strophomenacea having 4 prominent septa in the brachial valve ' (1956 : 859); and Strophomenidae: ' Strophomenacea having either normal or reversed convexity of the valves and a small foramen in the pedicle valve ' (1956 : 866). Thus, by those definitions, the only difference between a leptaenid and a strophomenid of normal convexity lies in the size of the foramen. As many species of *Leptaena* itself, e.g. *L. salopiensis* Williams, possess a foramen which is ' small, commonly sealed in adult shells ' (Williams 1963 : 461), this definition cannot be used in the type genus of the family. Even the geniculation and disc rugae may be seen on some genera, for example *Luhaia* Rõõmusoks 1956, ascribed to the Strophomeninae by Williams (1965 : H384).

However, there does occur a group of strophomenaceans which are normally geniculate and often possess rugae over most of the disc, and which may conveniently be grouped with *Leptaena* itself. But, bearing in mind the wide differences between the Strophomenidae, Christianiidae and Stropheodontidae, familial recognition as the Leptaenidae seems an unwarrantedly high taxonomic rank. In this paper they will be treated as a subfamily within the Strophomenidae, the Leptaeninae, although even this separation may not be valid, and some of the subfamilies may be inter-phyletic.

Although only three are considered in this paper, this arrangement leaves a total of seven subfamilies within the Strophomenidae, and their relative phylogenies leave much scope for discussion. Certainly the morphology of the two genera in the Leptaenoideinae, *Leptaenoidea* and *Leptaenisca*, seem to indicate descent from leptaenids rather than from other strophomenids, and this is supported by their known stratigraphical range.

Ecological occurrence

The species described in this paper are distributed as follows in the animal communities established in the British Llandovery (Ziegler 1965, Cocks 1967*a*, Ziegler, Cocks & Bambach 1968). The list omits *Leptaena urbana* Bancroft, whose community is unknown. No strophomenids have yet been found in the *Lingula* community, which is thought to have been the shallowest.

	Eocoelia Community	*Pentamerus* Community	*Stricklandia* Community	*Clorinda* Community
Pentlandina tartana Bancroft	—	—	×	×
Pentlandina parva Bancroft	—	—	—	×
Pentlandina parabola sp. nov.	—	—	—	×
Katastrophomena woodlandensis (Reed)	—	—	×	×
Katastrophomena scotica (Bancroft)	—	—	×	—
Katastrophomena penkillensis (Reed)	—	—	—	×
Leptaena martinensis sp. nov.	—	—	—	×
Leptaena haverfordensis Bancroft	—	—	×	×
Leptaena valida Bancroft	—	—	×	—
Leptaena contermina sp. nov.	×	—	×	—
Leptaena valentia sp. nov.	—	?	×	—
Leptaena zeta Lamont	—	—	—	×
Leptaena reedi sp. nov.	—	—	×	—
Leptaena ziegleri sp. nov.	—	—	×	—
Leptaena quadrata Bancroft	—	—	—	×
Leptaena purpurea sp. nov.	—	—	—	×
C. (Cyphomenoidea) wisgoriensis (Lamont & Gilbert)	—	×	×	?
C. (Laevicyphomena) feliciter sp. nov.	—	—	×	—
Mackerrovia lobatus (Lamont & Gilbert)	—	—	×	—

Family **STROPHOMENIDAE** King, 1846

Apart from the Leptaeninae, there are only two groups of Strophomenidae which have so far been found in rocks of Llandovery age, as recognized by Williams (1951 : 115), who at that time referred them provisionally to *Strophomena* Rafinesque and *Holtedahlina* Foerste.

The two groups are here referred to *Katastrophomena* gen. nov. and *Pentlandina* Bancroft 1949. These are placed in different subfamilies, the Furcitellinae and the Strophomeninae, and are the only post-Ordovician genera known in either subfamily. The chief subfamilial difference (Williams 1965 : H384, H386) is that the Strophomeninae are unequally parvicostellate and the Furcitellinae are costellate, but in fact later species of *Katastrophomena* (such as *K. penkillensis* (Reed) described below) become unequally parvicostellate. Thus in the two genera concerned, the chief differences in Silurian species lie in the internal structures of the brachial valve, and the usual presence of a strong fold and sulcus in *Pentlandina*.

Subfamily **STROPHOMENINAE** King, 1846

Genus ***PENTLANDINA*** Bancroft, 1949

1949. *Strophomena* (*Pentlandina*) Bancroft : 11, 13.
1965. *Pentlandina* Bancroft Williams : H384.
1966. *Pentlandina* Bancroft; Boucot *et al.* : 25.

Diagnosis: Biconvex to convexo-concave small stophomeninids with prominent fold and sulcus, often with an ornament of parvicostellae interrupting broken rugae.

Type species (by original designation); *Strophomena* (*Pentlandina*) *tartana* Bancroft 1949 from the Upper Llandovery of Deerhope Burn, Pentland Hills, Scotland.

Species assigned:

Strophomena (*Pentlandina*) *tartana* Bancroft 1949 : 13. Upper Llandovery, Pentland Hills, Scotland.

Strophomena (*Pentlandina*) *parva* Bancroft 1949 : 13, pl. 1, fig. 9. Upper Llandovery, The Frolic, Haverfordwest, Pembrokeshire.

Pentlandina parabola sp. nov. Upper Llandovery, Purple Shale, Shropshire.

Strophomena hirundo Barrande 1879, pl. 47, figs. 1–32 *pars*. Wenlock, Bohemia, Czechoslovakia.

Leptaena loveni de Verneuil 1848 : 339, pl. 4, fig. 5. Visby Marl (Upper Llandovery) Gotland, Sweden.

Leptaena parvula Kindle 1915 : 14, pl. 1, figs. 5–9. Stonewall Limestone, Saskatchewan, Canada.

Leptaena sinuosus Kindle 1915 : 13, pl. 1, figs. 1–4. Stonewall Limestone, Saskatchewan, Canada.

?Leptaena lewisii Davidson 1847 : 59, pl. 12, figs. 22–24, Lower Wenlock, Rushall Canal, Staffordshire.

Discussion. *Pentlandina* was raised to generic level by Williams (1965) and placed within the Strophomeninae. Boucot *et al.* (1966) recently removed the genus to the Leptaenidae on account of the pedicle muscle field and brachial processes and adductor plates (= trans-muscle septa?). It is, however, quite impossible to agree with this point, as each of the cited structures in *Pentlandina* is firmly attributable to the Strophomeninae rather than to the Leptaeninae. In fact the morphology of *Pentlandina tartana*, the type species described below, is not like any member of the leptaeninids. Taken with a shape so typical of the subfamily, there can be no doubt that the genus lies within the Strophomeninae. *Gunnarella* Spjeldnaes 1957 has a similar ornament to *Pentlandina*, but is geniculate as opposed to biconvex and sulcate.

Pentlandina tartana Bancroft

(Pl. 1, figs. 1–6)

1868. *Strophomena antiquata* (J. de C. Sowerby); Davidson : 17, pl. 2, figs. 21–23.
1871. *Strophomena antiquata* (J. de C. Sowerby); Davidson : 299 *pars*, pl. 44, figs. 7–9 only.
1949. *Strophomena* (*Pentlandina*) *tartana* [Lamont MS] Bancroft : 13, *non* pl. 1, fig. 10.

DIAGNOSIS: Small strophomeninid with prominent fold and sulcus. Fine ornament of differentiated parvicostellae which break irregular small weak rugae.

DESCRIPTION. *Exterior.* Biconvex to slightly resupinate with a semicircular outline and small ears. Large sulcus in pedicle valve with corresponding fold in brachial valve. Fine ornament of differentiated parvicostellae, and very weak irregular rugae of small wavelength distributed over all the shell. Interarea of variable size, larger in the pedicle than in the brachial valve. Large delthyrium closed at the apex by a small pseudodeltidium (Plate 1, fig. 4). Information uncertain as to the chilidium, there is at least a small one developed, but it is not clear whether or not part of the delthyrium remained open.

Pedicle interior. Straight hingeline with prominent teeth connected to the posterior end of a strong pair of short muscle bounding ridges which project anteriorly as much as dorsally. Short median septum starting close to the apex and dividing the muscle bounding ridges before stopping abruptly, leaving an inclined slope about 2 mm. long at its anterior end, which merges with the valve floor. Diductor scars short, leaving concentric growth ridges. Adductor scars elongate, close to, and partially on, the median septum. Shell thick posteriorly with prominent pseudopunctae, thin anteriorly, often with an interior reflection of the exterior ornament.

Brachial interior. Widely divergent prominent socket plates which curve slightly posteriorly at their lateral extremities. They are joined medianly to the bilobed cardinal process lobes, which are directed ventrally and slightly posteriorly. The process lobes are connected to a weak shaft, which in some specimens bifurcates anteriorly, in others reunites to form a weak median septum. Trans-muscle septa variably developed, but including in all specimens a prominent anterior pair stronger than and subparallel with the median septum. These septa are often slightly flared ventro-laterally. Owing to the mass of structures in the brachial valve presumably mainly used for the support of adductor muscles (although some could have been rudimentary brachiophore supports) the scars and shape of the muscles are not readily distinguishable. Thick shell with prominent taleolae antero-laterally.

LECTOTYPE (here selected). BB 31447 (Plate 1, figs. 1, 2), a brachial valve in the Davidson collection. One of a number of specimens which made up the material for the composite figures cited by Bancroft. With the specimens there is a label in Davidson's handwriting '*Strophomena antiquata* Sow. bed D. Wenlock Shale, Pentland Hills, found by Mr. Henderson.' The specimens are from an horizon now known to be of Upper Llandovery age in the North Esk Inlier of the Pentland Hills, Scotland (Mitchell & Mykura 1962 : 12 *et seq.*).

DIMENSIONS (in cm.—all specimens from type locality)

		l.	w.
BB 31447	Lectotype. Brachial valve .	0·91	approx. 1·6
B 8485	Brachial valve . . .	0·92	broken
BB 31450	Brachial valve . . .	0·86	1·39
B 13614	Pedicle valve . . .	0·72	1·29
BB 31448	Pedicle valve . . .	0·93	approx. 1·5

Discussion. In erecting the species, Bancroft (1949 : 13) quoted those of Davidson's figures of *Strophomena antiquata* which came from the Pentland Hills. He also figured a specimen (Plate 1, fig. 10) which is of part of a pedicle internal mould. This specimen is not in the Sedgwick Museum and Mr. A. G. Brighton informs me (*in litt.* March, 1967) that its whereabouts are unknown. In many copies of Bancroft's privately published paper, Dr. A. Lamont has deleted reference to the figure in the species description, and substituted '*S.* cf. *penkillensis*' as the caption for Plate 1, fig. 10, and indeed the specimen is probably of the latter species and may be attributed to *Katastrophomena* of the present paper. Thus, to stabilize the identity of *Pentlandina*, Davidson's figures have been selected as lectotypes of the type species by Havlíček (1968 : 75). The original specimens used by Davidson are selected above.

Apart from the Pentland Hills, the species has not been found in form identical with the type. There is, however, a larger form, represented as yet by only one pedicle and one brachial valve, probably attributable to *P. tartana*, found in one locality in the southern Welsh Borderland. This is at Cullimore's Quarry, Charfield Green, Gloucestershire, which lies in Tortworth Beds of C_6 age, part of the Tortworth Inlier. The dimensions are as follows (in cm.).

		l.	w.
BB 31470	Pedicle valve . . .	approx. 1·3	approx. 2·2
BB 31471	Brachial valve . . .	1·39	approx. 2·3

The larger size may well be a phenotypic feature, as there seem to be no differences in ornament, internal structures or general proportions between the Tortworth and Pentland Hills specimens.

Pentlandina parva Bancroft

(Pl. 1, figs. 7, 8)

1949. *Strophomena* (*Pentlandina*) *parva* Bancroft : 13, pl. 1, fig. 9.
1951. *Holtedahlina parva* (Bancroft) Williams : 118, pl. 7, figs. 8–10.

Discussion. A full description of the species is given by Williams (1951), and photographs of it are included in the present paper only for completeness and for comparison with *P. tartana* and *P. parabola*. The species is rare, it has so far been recorded only from the type locality, in Uzmaston Beds (Upper Llandovery) of the Frolic, south-west of Uzmaston Farm, Haverfordwest, Pembrokeshire. This is the same locality (Locality K of O. T. Jones on Sedgwick Museum labels) from which comes *Leptaena quadrata*, dealt with later in this paper, and it is interesting to note that neither species has been found except at the type locality.

To judge from the figures, the species seems to have a close relative in North America, the *P.* cf. *parva* of Boucot *et al.* (1966 : 25, pl. 6, figs. 16–18, pl. 7, figs. 1–10). The American species is, however, twice the size of the Welsh, no mention is made of any prominent fold and sulcus, and the arrangement of the brachial interior seems closer to *P. parabola* than to *P. parva*; all these features give a definite impression of specific difference.

Pentlandina parabola sp. nov.

(Pl. 1, figs. 9–12)

Diagnosis. Alate *Pentlandina* with pronounced fold and sulcus, and two pairs of converging muscle ridges in the brachial valve.

Description. *Exterior.* Outline semicircular but laterally alate. A deep ventral sulcus and dorsal fold are present, but lateral to these, minor frills are sometimes developed at the valve margin. Ornament of parvicostellae, with fine threads between them, more prominently developed in the median plane. New ribs arise by intercalation. In addition, small, even concentric rugae, broken by the parvicostellae are present, forming an irregular pattern. Medium-sized interarea, with an open delthyrium, bounded laterally by plates (Pl. 1, fig. 10) and a vestigial chilidium. Very small supra-apical foramen, atrophied in adult specimens and not always on the median plane.

Pedicle interior. Straight hingeline with prominent teeth which form the posterior end of a pair of muscle-bounding ridges of diamond shape, although they only sometimes meet at their anterior, enclosing a small diductor muscle scar which is weakly impressed. No information on the size and shape of the adductor muscle scars. Weak, broad median septum not extending anteriorly of the bounding ridges. Interior reflection of the ornament usually seen. Thin shell with no prominent taleolae showing.

Brachial interior. Divergent socket plates, curving antero-laterally. Small ventrally directed cardinal process lobes. Scarcely visible platform and weakly impressed muscle scars, but bounded laterally by two pairs of plates starting posteriorly at the lateral ends of the socket plates and set diagonally so that they converge anteriorly (but do not meet). Each plate is convex laterally and set at an angle to the valve floor. A very weak median septum runs for a short distance anterior of the bounding ridges.

Holotype. OUM C13507, a partly exfoliated pedicle valve from the Purple Shale (Upper Llandovery) of Domas, Shropshire. Grid Ref. SJ/5936 0062.

Dimensions (in cm.—all specimens from Domas)

		l.	w.
OUM C13507	Holotype Pedicle valve .	0·89	1·70
OUM C13504	Paratype Pedicle valve .	0·68	1·22
OUM C13505	Paratype Brachial valve .	broken	1·20
OUM C13509	Paratype Brachial valve .	0·26	0·51

Discussion. Length measurements were made in the median plane, but in old individuals there is some shell antero-laterally to this. In the small specimen (OUM C13509) the fold has not yet started to develop.

The species is known only from the Purple Shale of Shropshire and is rare, although it occurs as 2% of the population at the type locality. Single specimens are known

from two other localities, Boathouse Coppice [Grid. Ref. SJ/6205 0398] and Devil's Dingle [Grid Ref. SJ/6392 0547].

P. parabola differs from *P. parva* (Pl. 1, figs. 7, 8) in having a still more pronounced fold and sulcus, less distinct ornament and in better differentiated alae (without, however, being more transverse). In addition the strength, proportion and arrangement of the brachial internal structures are dissimilar in the two species. From *P. tartana* the new species differs in being more apsacline, more alate, and in having a frilly margin, in having a relatively smaller total muscle area and a differently shaped socket arrangement and muscle area in the brachial valve. In addition the rugae are more prominent, the interior less strongly papillose and the whole shell less thick.

Pentlandina sp.

(Pl. 1, fig. 13)

In one block from the Bog Mine, West Shropshire [Grid Ref. SO/3510 9815], there is a single broken pedicle valve, BB 31299, which may be referred without doubt to *Pentlandina*, on its general shape, particularly its prominent sulcus, and also on the character of the muscle field and bounding ridges. It seems fairly closely related to *Pentlandina parabola* but its shell is rather more irregular; in addition no trace of the distinctive ornament may be seen, but this could possibly be due to the coarse quartzite matrix. The length is 1·02 cm. and the estimated width approximately 1·6 cm.

The specimen is significant in being the earliest representative of the genus so far known, with an age of Middle Llandovery.

Subfamily **FURCITELLINAE** Williams, 1965

Genus ***KATASTROPHOMENA*** nov.

Diagnosis. Resupinate strophomenid with an ornament of irregular subequal costellae in early stocks, but may be parvicostellate in later stocks. With dental plates and weak trans-muscle septa.

Type species. *Strophomena antiquata* var. *woodlandensis* Reed 1917.

Species assigned:

Strophomena antiquata var. *woodlandensis* Reed 1917 : 902, pl. 18, figs. 20, 21, pl. 19, figs. 1–5. Middle Llandovery, Woodland Point, Girvan, Ayrshire, Scotland.

Orthis antiquata J. de C. Sowerby *in* Murchison 1839 : 630, pl. 13, fig. 13. Wenlock Shale, Woolhope, Herefordshire.

Strophomena dura Bancroft 1949 : 15, pl. 1, fig. 11, Wenlock Limestone.

Strophonella penkillensis Reed 1917 : 900, pl. 18, figs. 11–13. Upper Llandovery, Bargany Pond Burn, Girvan, Ayrshire.

Orthis scabrosa Davidson 1847 : 61, pl. 13, figs. 14, 15. Wenlock Limestone, Benthall Edge, Shropshire.

Strophomena scotica [and var. *alveata*] Bancroft 1949 : 12, pl. 1, figs. 4–7, *non* fig. 3. Gasworks Mudstone (Lower Llandovery) Haverfordwest, Pembrokeshire.

Strophomena woodlandensis geniculata [Bancroft MS *nom nud.*] Williams 1951 : 117, pl. 7, figs. 5–7. Upper Llandovery (C_1), Llandovery, Carmarthenshire.

Strophonella costatula Hall & Clarke 1894 : 359, pl. 84, figs. 15, 16. Niagara Group, Louisville, Kentucky, U.S.A.

Strophomena radiireticulata Twenhofel 1928 : 192, pl. 17, figs. 1–3. Jupiter Formation (Upper Llandovery-Wenlock), Anticosti Island, Canada.

?Strophomena sibirica Andreeva *in* Nikiforova & Andreeva 1961 : 183, pl. 38, figs. 1–7.

Species possibly congeneric:

Strophomena rugata Lindström 1860 : 371, pl. 13, fig. 14. Visby Marl (Upper Llandovery) Gotland, Sweden. (Possibly a young strophomenid).

Strophomena? pectenoides Andreeva *in* Nikiforova & Andreeva 1961 : 184, pl. 39, figs. 1–6. Middle Llandovery, Siberian Platform, U.S.S.R.

Strophomena lindstromi Gagel 1890 : 43, pl. 3, fig. 12, Upper Silurian, east Baltic. (May be a davidsoniacean).

Discussion. Unfortunately the genera of Upper Ordovician Strophomenidae have not yet been evaluated as a whole, and several are not yet comprehensively illustrated. It is probable, however, that the fairly compact group in the Silurian may be classified together in one genus to include all species not in *Pentlandina* or the Leptaeninae. All these species are resupinate and have a distinctive irregularly costate ornament, at least in the early Silurian. In addition, their internal characters, although often dissimilar at the specific level, clearly indicate their congeneric nature.

The new genus here erected to include these species is placed in the Furcitellinae, mainly owing to the similarities with *Furcitella* Cooper 1956 itself, particularly in the ornament and internal morphology, but the Chazy genus is biconvex and has a large foramen. Whether the two subfamilies Strophomeninae and Furcitellinae really require separation is another matter; the division (Williams 1965) seems to have been made mainly on ornamental grounds. In fact, although they are here left in separate subfamilies, *Katastrophomena* shows much resemblance to *Strophomena* itself in morphology, especially shape, differing mainly in the presence of dental plates and in the ornament, although, as mentioned above, *Katastrophomena* has end members with differentiated parvicostellae.

The only other strophomenid with which the new genus may be compared is *Microtrypa* Wilson 1945, from the Upper Ordovician of Ontario, Canada, which is particularly poorly known, but which appears to differ in ornament and brachial interior.

In the British Llandovery there are thus three species, *K. woodlandensis* and its subspecies *geniculata*, *K. scotica* and *K. penkillensis*, each of which will now be reviewed.

Katastrophomena woodlandensis (Reed)

(Pl. 2, figs. 1–10)

1883. *Strophomena antiquata* (J. de C. Sowerby); Davidson : 193, pl. 15, figs. 12–14.
1917. *Strophomena antiquata* (J. de C. Sowerby) var. *woodlandensis* Reed : 902, pl. 18, figs. 20, 21, pl. 19, figs. 1–5.
1949. *Strophomena woodlandensis* Reed Bancroft : 11.
1951. *Strophomena* aff. *woodlandensis* Reed; Williams : 118, pl. 7, fig. 4.

Diagnosis. *Katastrophomena* with coarse, irregular costae, variable shape, and variable brachial internal characteristics.

Description. *Exterior.* Variably resupinate, ranging from flat to almost geniculate. Ornament of thick irregular costae of subequal size. New costae arise mainly by intercalation, but sometimes by branching. Prominent growth lines seldom developed. Large interarea. Delthyrium completely closed by large pseudodeltidium and chilidium.

Pedicle interior. Straight hingeline with prominent teeth which form the posterior end of a pair of muscle-bounding ridges of variable shape but which generally curve inwards without meeting anteriorly. Median septum variably developed, on either side of which are faintly impressed blade-like adductor muscle scars inside the more strongly developed diductor scars upon which may be seen both faint concentric growth lines and also radiating striae. Fairly thick shell, particularly posteriorly, but large taleolae not developed.

Brachial interior. Strong pair of widely divergent socket plates quite separate from the small erect bilobed cardinal process. Very variable minor platform and muscle area structures (compare Pl. 2, fig. 6, 8, 9). A median septum is usually present, which bifurcates to a greater or lesser degree, trans-muscle septa are occasionally present.

Lectotype, here selected. B 54490, a pedicle valve, figured by Reed (1917, pl. 18, fig. 21) from the Middle Llandovery of Woodland Point, Girvan, Ayrshire, Scotland. Gray Collection.

Dimensions (in cm.—all specimens from Woodland Point)

		l.	w.
B 54490	Lectotype. Pedicle valve .	2·17	3·01
B 73012	Brachial valve . . .	2·05	3·17
BB 31420	Brachial valve . . .	1·54	2·25
BB 31422	Brachial valve . . .	1·78	2·37

Discussion. There is a large amount of variability in *Katastrophomena woodlandensis*, particularly in two respects; the degree of valve convexity, and the development of internal brachial structures. Both points may be seen in Pl. 2; where figs. 5–7 show specimens in which the valve direction has changed in the median plane by more than 90 degrees, whereas figs. 8 and 9 show specimens which are only slightly concave. Similarly the contrast in the brachial interiors between figs. 8 and 9 is self-evident.

K. woodlandensis is not common except at the type locality, but the species is also present in the Middle Llandovery of the type area. Two specimens have been found, SMA 30006 (Williams 1951 : 118, pl. 7, fig. 4) and BB 31409, collected by the author from B_3 mudstones in a small disused roadside quarry [Grid Ref. SN/760 309].

A subspecies has also been erected, *K. woodlandensis geniculata* [Bancroft 1949 *nom nud.*] Williams (1951 : 117, pl. 7, figs. 5–7), whose type specimens are refigured here for convenience (pl. 3, figs. 1, 2). This is another rare form from C_1 beds in the Llandovery area. It is best left as a separate subspecies, as, although the brachial valve could well be identified as *K. woodlandensis* (s. s.), the form of the pedicle muscle field shows some affinity with *K. scotica* described below. Further collecting at the type locality has failed to produce more material.

The chief differences between *K. woodlandensis* and *K. scotica* are in the shapes of the pedicle muscle field and bounding ridges and in the stronger median septum usually present in *K. scotica*. The chief difference between these two species and *K. penkillensis* lies in the differentiated ornament of the latter.

Katastrophomena scotica (Bancroft)

(Pl. 3, figs. 3–9)

1871. *Strophomena antiquata* (J. de C. Sowerby); Davidson *pars* : 299, pl. 44, figs. 21, 22 only.
1949. *Strophomena scotica* Bancroft : 12, pl. 1, figs. 4, 5, *non* fig. 3.
1949. *Strophomena scotica* var. *alveata* Bancroft : 13, pl. 1, figs. 6, 7.
1951. *Strophomena scotica* Bancroft; Williams : 116, pl. 7, figs. 1–3.

Diagnosis. *Katastrophomena* with irregular costae. Pedicle muscle field diamond-shaped posteriorly with bounding ridges drawing out anteriorly to become sub-parallel in extreme cases.

Description. *Exterior.* Variably resupinate. Ornament of thick, irregular costae of subequal size. New costae arise by bifurcation and intercalation. Prominent concentric growth-lines often developed. Large interarea, with at least a small pseudodeltidium and possibly a large, entire one. Large chilidium.

Pedicle interior. Straight hingeline with prominent teeth which form the posterior end of a pair of variably developed muscle bounding ridges of curved to diamond shape, not meeting anteriorly, but sometimes drawn out and extending sub-parallel for a short distance anteriorly. Weak median septum running from the apex to approximately the ends of the muscle bounding ridges. On either side of this septum are sometimes impressed the pair of small blade-like adductor muscle scars. Strongly impressed diductor muscle scars on which concentric growth lines are often seen.

Brachial interior. Large pair of strongly divergent socket plates on either side of, and distinct from, the erect bilobed cardinal process. Between the lobes is sometimes preserved a small thin blade. Median septum usually strong, variably bifurcate. Other structures very variable, trans-muscle septa and muscle bounding ridges are sometimes weakly developed.

LECTOTYPE, here selected. SMA 32194, a pedicle internal mould, figured Bancroft (1949, pl. 1, fig. 4) from the Gasworks Mudstone (Lower Llandovery), cutting opposite entrance to gasworks, Haverfordwest, Pembrokeshire. Turnbull Collection.

DIMENSIONS (in cm.—all specimens from type locality)

		l.	w.
SMA 32194	Lectotype, pedicle valve .	2·62	approx. 3·7
SMA 32193	Pedicle valve . . .	2·46	approx. 3·5
BB 31435	Pedicle valve . . .	2·21	3·05
BB 31412	Brachial valve . . .	2·35	approx. 2·8
BB 31443	Brachial valve . . .	0·90	1·23

DISCUSSION. The second specimen figured by Bancroft has been chosen as lectotype because the first (1949, pl. 1, fig. 3) is the counterpart to the figured example of '*Strophomena*' *agrestis* from the Slade Beds (SMA 32040), and was presumably illustrated as *S. scotica* in error. Bancroft also erected a variety, *S. scotica* var. *alveata*, without giving any differences from the nominal subspecies. As the localities are the same and the types of both subspecies virtually identical (refigured here Pl. 3, figs. 4–8) and within the range of variation found in the Gasworks Mudstone, no subspecies of *K. scotica* seem necessary.

Williams (1951 : 116) selected a specimen from the Gasworks Mudstone of the Frolic section as type for the species, but as this is not one of Bancroft's originals the selection is not valid. Williams' specimen (refigured here Pl. 3, fig. 9) is, however, clearly conspecific with the type material from the entrance to the gasworks at Haverfordwest.

Katastrophomena penkillensis (Reed)

(Pl. 4, figs. 1–6)

?1871. *Strophomena antiquata* (J. de C. Sowerby); Davidson *pars* pl. 44, fig. 5 only.
1917. *Strophonella penkillensis* Reed : 900, pl. 18, figs. 11–14.

DIAGNOSIS. *Katastrophomena* with differentiated parvicostellate ornament.

DESCRIPTION. *Exterior.* Gently resupinate. Ornament of fairly fine differentiated parvicostellae, the smaller type mere threads. New ribs arise by intercalation. Large ventral interarea, but smaller on brachial valve than other species of the genus. No information on extent of pseudodeltidium. Chilidium present. Occasional prominent growth lines sometimes seen on valve exterior.

Pedicle interior. Straight hingeline with prominent teeth which form the posterior end of a pair of muscle bounding ridges of approximately diamond shape, although they do not meet anteriorly. Median septum running from the apex to a position level with, or just anterior to, the ends of the muscle bounding ridges. On either side of the anterior end of the septum are a pair of bladelike adductor scars, which themselves may run anterior to the end of the bounding ridges. Diductor scars strongly impressed, sometimes with radiating striae and concentric growth ridges. Shell of variable thickness with large postero-median taleolae not developed.

Brachial interior. Fairly straight socket plates widely divergent. Normal erect bilobed cardinal process. Variably developed muscle field structures; trans-muscle septa sometimes seen (Pl. 4, fig. 3, but not in Pl. 4, fig. 1). Broad, faint platform between two more or less circular muscle scars which are weakly impressed.

Lectotype (here selected) B 73013, a brachial internal mould, figured by Reed (1917, pl. 18, fig. 11) from the Upper Llandovery of Bargany Pond Burn, Girvan, Ayrshire, Scotland. Gray Collection.

Dimensions (in cm.—all specimens from Bargany Pond Burn)

		l.	w.
B 73013	Lectotype, brachial valve .	1·57	2·74
BB 31432	Brachial valve . . .	1·15	approx. 2·3
BB 31472	Pedicle valve . . .	1·40	2·86

Discussion. Despite the localities being given by Reed as (1) Penkill (2) Bargany Pond Burn, all his figured specimens come from Bargany Pond Burn, where the species is, however, rare. Reed put the species into *Strophonella* as he described the hingeline as ' finely crenulated ', but there is no doubt that the hingelines of the specimens to hand, which include all Reed's syntypes, are smooth. It is surprising that Reed made this mistake, especially as Davidson had already labelled some of the specimens as *S. antiquata* (*fide* Reed 1917 : 901, no Davidson label is with the type lot today).

Katastrophomena penkillensis also occurs rarely in the higher Llandovery horizons in Shropshire, for example a pedicle valve (BB 31408) from the Minsterley Formation (pl. 4, fig. 6) and a brachial valve from the Purple Shale of the Onny River, GSM 11693.

Thus so far the species seems confined to the top half of the Upper Llandovery, and to judge both from their ornament and general aspect, it is probable that the Wenlock species of the genus were derived direct from some earlier form such as *K. woodlandensis* rather than from *K. penkillensis*, despite its wide geographical range.

Katastrophomena sp.

(Pl. 4, figs. 7, 8)

In the material from Shropshire there are, in addition to the specimens of *K. penkillensis* from the upper beds, two brachiopods referable to *Katastrophomena* from the lower horizons in the northern Longmynd-Shelve outcrop. These consist of a pedicle valve from the Venusbank Formation of The Corners, near Betton [Grid Ref. SJ/314 025] and a brachial valve from the Bog Quartzite of Bog Mine [Grid Ref. SO/3510 9815]. The latter is poorly preserved (BB 31451, Pl. 4, fig. 7), but clearly shows the furcitellinid bifurcation of the median septum. The pedicle valve (BB 31407, Pl. 4, fig. 8) is a large specimen for the genus and has a more angularly pentagonal muscle field than the contemporary *K. woodlandensis geniculata*, perhaps more similar to some specimens of *K. scotica* from the Lower Llandovery;

however the short median ridge does not extend anteriorly of the muscle bounding ridges as in the latter species.

There is no doubt as to the generic identity of these Shropshire specimens, and thus they are provisionally described here until more material comes to light. Both specimens show marked differences from the named species of *Katastrophomena*. It is noteworthy that no material ascribable to this genus has so far come to light in any part of the southern Welsh Borderland.

Subfamily **LEPTAENINAE** Hall & Clarke, 1894

The relationships and status of the leptaenids have been discussed above under the heading of the superfamily. Three genera attributable to the subfamily have been found in the British Lower Silurian, *Leptaena*, *Cyphomena* and *Mackerrovia* gen. nov. A fourth genus, *Bellimurina*, is represented by a single specimen. It is possible that some species here treated as *Leptaena* might be put into such later genera as *Bracteoleptaena* Havlíček 1963 from the Bohemian Wenlock, but in the Llandovery the variation is not enough to separate such species from *Leptaena* itself.

Genus ***LEPTAENA*** Dalman, 1828

Type species. *L. rugosa* Dalman 1828 from the Upper Ordovician Dalmanitina Beds of Få dalaberg, Västergötland, Sweden. A lectotype was selected and the species figured by Spjeldnaes (1957, p. 173, pl. 7, figs. 1, 2, 4), and also by Williams (1965, fig. 252, figs. 5a, 5b).

The species problem in *Leptaena* seems more acute than in most other genera of brachiopods. After the mid-Ordovician radiation, the subfamily Leptaeninae grew smaller in terms of generic numbers, and thus by Llandovery times the genera were reduced to approximately five, and all save *Leptaena* itself are rare and sporadic. On the other hand there is some variation in the form of *Leptaena* between nearly every locality in which one finds it. This bears out the assertion of Imbrie (1956, p. 219): ' Study of living populations has shown that if sufficiently rigorous methods are employed, significant morphological and genetic differences between two populations can be demonstrated. Hence species and subspecies must be considered as collective categories, in the sense that they are composed of local populations no two of which are identical.'

Thus a very large number of specific or subspecific names could have been erected in the present work, but these would have served only as a smokescreen to hide the basic truth of the ' *Leptaena rhomboidalis* ' concept. Here was a successful stock, essentially unchanged from the Ordovician to the Carboniferous, which remained firmly established in an apparent variety of ecological niches.

However there are some differences upon which species have already been erected, and in many of these cases the differences do persist in many populations from many localities. Thus their taxonomic expression is a positive step towards their recognition and understanding.

Havlíček (1968) has referred several Silurian species to *Leptagonia* on the grounds that their morphogeny has proceeded nearer that genus than to typical *Leptaena*. In this paper all the Silurian forms are retained in *Leptaena* until the Devonian and Carboniferous stocks become better known.

There now follows a list of previously erected species of *Leptaena* of Ashgill, Llandovery and Wenlock age, followed by a list of species previously referred to the genus, but which are here considered distinct from it.

Ashgill and Silurian species assigned.

Leptaena rugosa Dalman 1828 : 106, pl. 1, fig. 1. Dalmanitina Beds (Ashgill) of Västergötland, Sweden.

Anomites rhomboidalis Wahlenberg 1821 : 65. ?Wenlock of North German drift.

Producta depressa J. de C. Sowerby 1823 : 86, pl. 459, fig. 3. Wenlock Limestone of Dudley.

Leptaena tenuistriata J. de C. Sowerby *in* Murchison 1830 : 636, pl. 22, fig. 2. Wenlock of Marloes Bay, Pembrokeshire.

Leptaena depressa var. *vulgaris* Barrande 1848 : 84, pl. 22, figs. 6, 7. Wenlock/Ludlow of Bohemia, Czechoslovakia.

L. quadrilatera Shaler 1865 : 65. Ellis Bay Formation, Anticosti Island, Canada.

L. schmidti Gagel 1890 : 50, pl. 5, fig. 28. Lyckholm Fm (Upper Ordovician) East Baltic.

L. richmondensis Foerste 1909 : 211, pl. 4, fig. 10. Richmond Group, Ohio, U.S.A.

L. richmondensis var. *precursor* Foerste 1909 : 211, pl. 4, fig. 11. Richmond Group, Ohio, U.S.A.

L. rhomboidalis ' var. β ' Reed 1917 : 872, pl. 13, fig. 1. Whitehouse Group, Girvan, Ayrshire.

L. rhomboidalis 'var. γ ' Reed 1917 : 872, pl. 13, figs. 2, 3. Drummuck Group, Girvan, Ayrshire.

L. rhomboidalis ' var. δ ' Reed 1917 : 872, pl. 13, fig. 4. Mulloch Hill Sandstone (Lower Llandovery), Girvan, Ayrshire. (Here described as *L. valentia mullochensis*.)

L. rhomboidalis ' var. ϵ ' Reed 1917 : 872, pl. 13, figs. 5, 6, *non* fig. 7. Woodland Point (Middle Llandovery), Girvan, Ayrshire. (Here described as *L. valentia* sp. nov.)

L. rhomboidalis var. *nana* Chernychev 1937 : 67, pl. 2, figs. 16–18. Wenlock of Mongolia.

L. zeta Lamont 1947 : 200. Penkill Group (Upper Llandovery), Girvan, Ayrshire.

L. haverfordensis (and var. *contracta*) Bancroft 1949 : 6, pl. 1, figs. 18–24. Gasworks Mudstone (Lower Llandovery), Haverfordwest, Pembrokeshire.

L. valida Bancroft 1949 : 6, pl. 1, fig. 25. Upper Llandovery (C_1), Llandovery, Carmarthenshire.

L. urbana Bancroft 1949 : 6, pl. 2, figs. 1, 2. Upper Llandovery (C_4), Llandovery, Carmarthenshire.

L. elongata Bancroft 1949 : 7, pl. 1, figs. 26, 27. Upper Llandovery (C_1), Llandovery, Carmarthenshire.

L. quadrata Bancroft 1949 : 7, pl. 1, figs. 28–30. Upper Llandovery, The Frolic, Haverfordwest, Pembrokeshire.

L. ? tennesseensis Amsden 1949 : 54, pl. 5, figs. 11–15. Brownsport Formation (Wenlock/Ludlow), U.S.A.

L. delicata Amsden 1949 : 55, pl. 5, figs. 11–15. Brownsport Formation (Wenlock/Ludlow), U.S.A.

L. oklahomensis Amsden 1951 : 85, pl. 16, figs. 29–35. Henryhouse Formation (Wenlock/Ludlow), U.S.A.

L. acuteplicata Sokolskaya 1954 : 60, pl. 4, figs. 1–4. Porkuni Stage (Upper Llandovery), Estonia, U.S.S.R.

? Productus twamleyii Davidson 1848 : 315, pl. 3, fig. 1. Wenlock Limestone, Dudley, Worcestershire. [The original specimen is not now to be found, but Davidson (1871 : 282) later put the species into synonymy with *L. rhomboidalis*.]

Species excluded from Leptaena

Leptaena sinuosus and *L. parvula* Kindle 1915. See *Pentlandina*.

L. wisgoriensis Lamont & Gilbert 1945. See *Cyphomena*.

L. centervillensis Foerste 1923. Brassfield Limestone, Ohio.

L. julia (Billings 1862). See *Cyphomena*.

L. loveni de Verneuil 1848. See *Pentlandina*.

L. bella Williams 1951 : 119, pl. 7, figs. 14, 15. Middle Llandovery, Llandovery. Probably an undescribed genus, but the small amount of material at present available does not warrant redescription.

Three groups within *Leptaena* are recognizable in the British Llandovery.

(a) Large species with more or less oval-sided pedicle muscle scars.

(b) Large species with more or less parallel-sided pedicle muscle scars.

(c) Small species, which as at present known are a rather less well-knit group than either of the other two, and which will probably be found to be an amalgam of further groups when more material becomes available.

In the Lower and Middle Llandovery the first two groups of species seem to have been confined to the Scottish area and the Anglo-Welsh area respectively, and this remains substantially true for the Upper Llandovery, but in late Upper Llandovery time there was some admixture of the two groups; thus rare *L. zeta* occurs in the Purple Shale of Shropshire, and the leptaenid found in Deerhope Burn has the oval muscle-scar outline.

The first two groups could thus have shared a mutual ecological niche, as they have not so far been found occurring together. On the other hand, representatives of the third group, the small species, do sometimes occur with members of one or other of the larger groups, examples of this being at Woodland Point, Girvan, where *L. valentia* and *L. reedi* occur side by side in apparent harmony, and at locality H-G-A in the Malverns where *L. contermina* and *L. ziegleri* also occur together. Thus at least two separate ecological niches may be inferred for species of *Leptaena* in level bottom communities at this time, although for the most part only one or other of them was occupied, and the genus is absent from many localities.

Whether this scheme holds good for other parts of the world during the Lower Silurian has not yet been established. The only foreign species of *Leptaena* so far

described from beds of Llandovery age, *L. acuteplicata* Sokolskaya 1954 from Estonia, has not yet been illustrated with interior views, so that its relationship with British species remains unknown.

Some consideration has been given to the possibility of formal subgeneric recognition of the three groups, but this has been withheld as taxonomic splitting of this kind does not seem justified in a generic group which remains extremely well-knit, and whose phylogeny is at the moment not completely understood, although some relationships are clear. Another possibility would be to have one species name for each of the groups, with various subspecies, but this would unite the various small forms of the third group under one specific name, which would certainly obscure the true situation, in which most of them are definitely more than subspecifically separable.

The British Llandovery species will now be described in the three groups as follows:

(a) *L. martinensis* sp. nov., *L. haverfordensis* Bancroft 1949, *L. valida* Bancroft 1949, *L. urbana* Bancroft 1949, *L. contermina* sp. nov.
(b) *L. valentia* sp. nov., *L. valentia mullochensis* subsp. nov., *L. zeta* Lamont 1947.
(c) *L. reedi* sp. nov., *L. ziegleri* sp. nov., *L. quadrata* Bancroft 1949, *L. purpurea* sp. nov.

Their possible phylogeny is shown in Text-fig. 1.

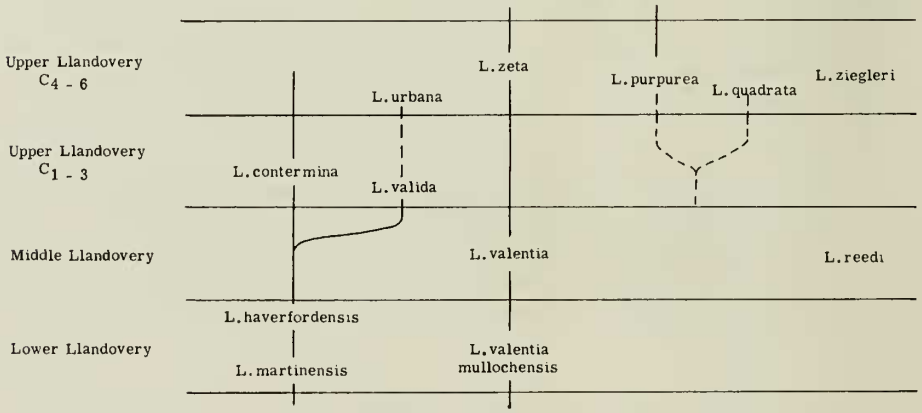

FIG. 1.

Leptaena martinensis sp. nov.

(Pl. 4, figs. 9–13, Pl. 5, figs. 1–3)

?1949. *Leptaena martini* Bancroft : 6, *non.* pl. 1, fig. 18 *nomen nudum.*

DIAGNOSIS. *Leptaena* with strong rugae and well defined ornament. Poorly developed muscle bounding ridges of variable shape.

DESCRIPTION. *Exterior.* Shape semicircular to quadrate with alae. Geniculation between 70 and 90 degrees. Ornament of well-defined, subequal parvicos-

tellae. Rugae strong with a particularly large ruga at the knee. Small interarea with delthyrium mainly closed by a small chilidium. No information on the foramen, but probably small.

Pedicle interior. Widely divergent teeth with fairly prominent thin dental plates. Muscle bounding ridges are poorly developed for the genus and of variable shape, sometimes oval, sometimes angular; they do not meet anteriorly. No information on the shape of the adductor scars which are not impressed at all on the material to hand. No median septum. Central talaeolae, though not large, are more prominent than on the trail.

Brachial interior. Large divergent cardinal process lobes, mounted on a platform. The postero-lateral parts of the latter serve as the anterior ends of the sockets. The platform is trilobed anteriorly, partly enclosed subcircular adductor muscle scars. Median septum usually absent, but in a few specimens a very faint ridge may be seen about halfway to the edge of the disc. Occasional prominent pseudopunctae in the central region outside the muscle field.

Holotype. SMA 31865 a pedicle valve (both interior and exterior are preserved) from Cartlett Beds (Lower Llandovery), St. Martin's Cemetery, Haverfordwest, Pembroke. Turnbull Collection.

Dimensions (in cm.—all specimens from St. Martin's Cemetery). Note that in all the following measurements of species of *Leptaena* the term l_d signifies the distance from the umbo to the knee measured along the median plane; as the trail of the various species differs so much, both in form and angle with the disc, a normal measurement of length is meaningless for comparative purposes.

		l_d	w.
SMA 31865	Holotype pedicle valve .	1·50	approx. 3·2
SMA 31859	Paratype pedicle valve .	0·62	1·22
SMA 31860	Paratype pedicle valve .	0·97	2·04
SMA 31864	Paratype brachial valve .	1·68	approx. 3·3
SMA 31861	Paratype brachial valve .	0·53	approx. 0·9

Discussion. In his paper, Bancroft (1949 : 6) erected '*Leptaena martini* sp. nov.' giving St. Martin's Cemetery as the type locality, but referring the reader to his pl. 1, figs. 18, 23. These two figures are, in fact, of *L. haverfordensis* from the Gasworks Mudstone of the gasworks, Haverfordwest (SMA 32161 and 40512). Thus the species is without illustration, or reference to a previous illustration, and thus a *nomen nudum*, according to the rules of nomenclature. Bancroft mentions two species present at the St. Martin's Cemetery, a large one and a small one, but this is not borne out by the material in the Turnbull Collection or in subsequent collections made by the author. Possibly Bancroft was misled by the small individuals present in the Turnbull Collection, but these are all immature as shown by the lack of geniculation (pl. 5, figs. 1–3).

The Cartlett Mudstones are the oldest representatives of the Silurian in South Wales, and indeed almost certainly span the Ordovician-Silurian boundary, as the

writer has found *Tretaspis* at their base (kindly confirmed by Dr. W. T. Dean) in a temporary (1965) exposure in the foundations for a housing estate behind St. Martin's Cemetery itself.

L. martinensis is probably an ancestor of *L. haverfordensis*, but differs from it in the more prominent ornament and rugae, and in the more variably shaped and less developed pedicle valve muscle bounding ridges.

Leptaena haverfordensis Bancroft

(Pl. 5, figs. 4–15)

1949. *Leptaena haverfordensis* Bancroft : 6, pl. 1, figs. 19–20, 23, 24.
1949. *Leptaena haverfordensis* var. *contracta* Bancroft : 6, pl. 1, figs. 18, 21–22.

Diagnosis. Large *Leptaena* with oval-sided pedicle valve muscle area. Socket plates variably present.

Description. *Exterior.* Shape semicircular with alae. Angle of geniculation between 75 and 90 degrees. Ornament of numerous fine but well-pronounced, sub-equal parvicostellae. Well-developed regular rugae, of relatively small wave length for the genus (observed range on the pedicle valve = 10–15 in adult specimens). At the knee there is always a prominent ruga and just posterior to this an unusually pronounced trough. One or two rugae sometimes seen on the upper half of the trail. Medium-sized interarea; no information on foramen, but probably small.

Pedicle interior. Prominent teeth and dental plates merging with muscle bounding ridges of oval shape; these flare outwards from the valve floor and sometimes meet anteriorly, and sometimes are open. Prominent pair of lanceolate adductor scars between the diductor scars which often have prominent radiating striae across them. Median septum not developed except as a ridge dividing the muscles. Prominent taleolae sometimes developed centrally outside the muscle field.

Brachial interior. Prominent erect slightly divergent cardinal process lobes between widely divergent socket plates. Irregular platform developed often trilobed anteriorly to enclose the pair of suboral adductor scars. The central lobe extends further anteriorly to form a very thin, usually faint, median septum. Prominent taleolae on the disc outside the muscle field.

Lectotype, here designated. SMA 32163 a pedical valve (figured Bancroft 1949, pl. 1, fig. 20) from the Gasworks Mudstone (Lower Llandovery) opposite entrance to the gasworks, Haverfordwest, Pembrokeshire.

Dimensions (in cm.)		l_d	w.
SMA 32163	Lectotype, pedicle valve .	2·21	approx. 3·5
BB 31355	Pedical valve . . .	1·60	2·96
BB 31326	Pedicle valve . . .	1·54	3·45
BB 31363	Brachial valve . . .	1·63	approx. 2·6
BB 31341	Brachial valve . . .	1·84	approx. 3·4

Discussion. Bancroft erected *L. haverfordensis* var. *contracta* from the same locality, based on a single specimen (SMA 40512) which is refigured here (Pl. 5, fig. 14). From large collections made from the Gasworks Mudstone, it is clear that there are all intergrades between this specimen, with its well impressed musculature and vascular system, and the typical form, so that no sub-species seems warranted.

The species occurs in the Lower Llandovery of Pembrokeshire and also in the type area of Llandovery, but has not yet been discovered elsewhere, which is not very surprising as these two areas represent the most fossiliferous Lower Llandovery in the Welsh area. In Girvan, the same ecological niche was occupied at this time by *Leptaena valentia mullochensis* subsp. nov.

Leptaena valida Bancroft

(Pl. 6, figs. 1–5)

1949. *Leptaena valida* Bancroft : 6, pl. 1, fig. 25.
1949. *Leptaena elongata* Bancroft : 7 pl. 1, figs. 26, 27.

Diagnosis. Large *Leptaena* with oval-sided pedicle muscle field which may be bilobed anteriorly. A few larger parvicostellae antero-medianly.

Lectotype, here selected. SMA 35690, a pedicle valve, external and internal mould (figured by Bancroft 1949, pl. 1, fig. 25) from C_1 beds (Upper Llandovery), O. T. Jones collection, his locality 26 SE/E λ13, River Sefin, 400 yards south-east of Llety'r-hyddod, Llandovery, Carmarthenshire.

Dimensions (in cm.)	l_d	w.
SMA 35690 Lectotype, pedicle valve .	1·20	approx. 4·3
SMA 35691 Pedicle valve . . .	1·83	—

Discussion. The specimen of *Leptaena valida*, one pedicle valve, and the specimens of *L. elongata*, two pedicle valves, both come from the same locality, i.e. the C_1 shales full of *Stricklandia lens progressa* by the side of the River Sefin, Llandovery. All are clearly the same species, but the lectotype has been preserved with its disc oblique to the bedding plane, and has thus been distorted to give a greater apparent width than the other two specimens. Subsequent collecting at the locality has resulted in another crushed pedicle valve, but the brachial valve is still unknown.

The species is striking in that several parvicostellae are distinctly larger than the rest in the antero-median region of the valve, giving an impression of differentiation over this small area only.

Leptaena urbana Bancroft

(Pl. 6, figs. 6, 7)

1949. *Leptaena urbana* Bancroft : 6, pl. 2, figs. 1, 2.

Lectotype, here selected. SMA 35693 a pedicle internal mould, (figured Bancroft 1949 pl. 2, fig. 1) from C_1 Beds (Upper Llandovery), O. T. Jones collection,

his locality 27 NW/E λ8, quarry 500 yards north-east of Cefn Cerig, Llandovery, Carmarthenshire.

Dimensions (in cm.)	l_d	w.
SMA 35693 Lectotype, pedicle valve .	approx. 2·5	approx. 4·2
SMA 35694 Brachial valve . . .	2·25	approx. 4·5

Discussion. The two specimens figured by Bancroft are the only representatives of the species in the Sedgwick Museum and further collecting from the type locality has not produced more material.

The species is distinct in its pedicle muscle field shape and size and in the weakness and irregularity of its rugae. It thus appears to have a valid specific concept, but in the absence of more material, further consideration to it will not be given here.

Leptaena contermina sp. nov.

(Pl. 6, figs. 8–13, Pl. 7, figs. 1–11)

1871. *Strophomena rhomboidalis* (Wilckens); Davidson, pl. 39, fig. 17 only.

Diagnosis. Transverse *Leptaena* with interior encircling ridges in both valves, and regular rugae.

Description. *Exterior.* Mucronate and sharply geniculate. Apart from the large ears, the shell shape is approximately semicircular, although rather transverse. Equally parvicostellate ornament, with ribs increasing slightly in size anteriorly. Occasionally new ribs arise either by intercalation or more commonly by bifurcating (OUM C9153 shows both methods on a single brachial valve, an external mould). Rugae regular and continuous. The number of rugae on the disc varies between six and ten within a population. The geniculation occurs at different lengths within a population, but usually between 1·0 and 1·4 cm. The angle between the disc and trail is between 75 and 90 degrees. Open delthyrium, prominent chilidium. The pedicle foramen has not been observed on any specimen.

Pedicle interior. Teeth and dental plates small for the genus and fused to a small anterior extension of the hingeline. Large, prominent and evenly curving muscle boundary ridges, nearly meeting anteriorly and fusing posteriorly with an extension of the dental plates. A small median ridge divides the lanceolate adductor scars, which are usually very poorly impressed. In some specimens, the diductors completely enclose the adductors, in others they just fail to do so. Striae are developed on the muscle field, particularly on the diductors. The more coarsely pustulate disc and some of the trail are bounded by a nearly semicircular ridge which runs round the trail anteriorly but laterally crosses the geniculation and merges posteriorly with the hingeline at a low angle near the dental plates. The internal reflection of the ornament is much stronger outside this ridge. Coarse pseudopunctae posteromedianly, except on the muscle field, but not so prominent as in the brachial valve.

Brachial interior. Cardinal process lobes prominent, between them a much smaller narrow blade-like process. Socket plates variably developed and widely divergent, with rarely-preserved striae on their anterior side. Running anteriorly and laterally is a three pronged platform which bounds the posterior edge of the

adductor scars, and the middle prong of which divides them, forming a short, broad median ridge. This line is marked discontinuously anteriorly as a fine ridge until near the edge of the disc, and in many specimens is more pronounced near its anterior end. As with the ventral valve a ridge runs laterally from the hingeline posterior of the sockets to the edge of the disc, but instead of crossing the geniculation as with the pedicle valve, it stays on its edge, thus making a wall on the anterior edge of the brachial valve which is not reflected on the exterior. Except in the muscle field, there are prominent pseudopunctae which are random posteriorly, but anteriorly are arranged in lines parallel to the external ornament. They are smaller and less well defined outside the encircling ridge.

Holotype. OUM C9168 a pedicle valve from the Venusbank Formation (Middle Llandovery), Hope Quarry, Shropshire. Grid Ref. SJ/3551 0208. Author's collection.

Dimensions (in cm.)			l_d	w.
OUM C9168	Holotype, pedicle valve	Hope Quarry	1·21	2·24
OUM C9155	Paratype, brachial valve	Hope Quarry	1·11	—
OUM C10501	Paratype, brachial valve	Bog Mine	1·17	2·90
BB 31280	Paratype, pedicle valve	Bog Mine	1·34	2·81
BB 31289	Paratype, pedicle valve	Bog Mine	1·24	2·46

Discussion. There is no mistaking this species from any yet described. It is much more transverse than most species of *Leptaena*, and the rugosity is much more regular than average, yet not obscuring the ornament. As may be seen from the illustrations, there is some variation of the muscle pattern and relative dimensions, but the species is extremely homogeneous between the various localities.

Its nearest probable relative is *L. haverfordensis* from the Gasworks Mudstone, which it resembles in the general configuration of the muscle pattern (except in the strength of the adductor scars), but it does not have the raised rim to the disc of that species, nor is the rugae pattern the same. From *L. valida* and *L. quadrata* and *L. urbana*, all from the Upper Llandovery, it differs in diductor muscle configuration, rugae pattern, and also in ornament, the first two species having more prominant costellae near the median plane, and the third being almost without ornament. From the later, Wenlock, species it differs in the relative shortness and regularity of its trail, the presence of the ventral encircling ridge, and the less massive teeth and chilidium.

In Shropshire the species is confined to the Bog Quartzite and Venusbank Formation. It also occurs in the Cowleigh Park Beds of the Malverns, the Wych Beds of the Malverns and the Yartleton Beds of May Hill, the last two occurrences being substantially the younger.

Leptaena valentia sp. nov.

(Pl. 8, figs. 1–8)

1917. *Leptaena rhomboidalis* (Wilckens) var. *ε* Reed : 872, pl. 13, figs. 5, 6 *non* fig. 7.

Diagnosis. Large *Leptaena* with sub-parallel muscle bounding ridges.

Description. *Exterior.* Shape semicircular with more or less prominent alae. Geniculation between 70 and 90 degrees. Ornament of subequal parvicostellae, which arise by bifurcation or intercalation. Rugae fairly regular, with a particularly large ruga developed at the knee. Medium-sized interarea with prominent growth lines. Delthyrium almost entirely closed by the large chilidium, but there is a very small pseudodeltidium at the delthyrial apex. Foramen not seen, but probably small and closed.

Pedicle interior. Fairly small grooved teeth and dental plates for the genus, the latter joined to a pair of strong muscle bounding ridges which flare outwards from the valve floor. The form of the bounding ridges is variable, but they usually diverge widely posteriorly with the socket plates, then change direction sharply by up to 45 degrees becoming subparallel, continuing anteriorly until they merge with the valve floor from between half and two-thirds way to the knee. The two bounding ridges never meet. Very small median ridge on either side of which are the poorly impressed lanceolate adductor scars. The diductor muscle scars are strongly impressed within the bounding ridges and often have striae impressed upon them. Coarsely pustulate in the central region of the valve, outside the muscle area.

Brachial interior. Prominent, erect, bilobed cardinal process, the two lobes diverging slightly laterally. Immediately anterior to these is a prominent platform consisting of a pad of secondary calcite. The posterior edge of the pad on either side of the cardinal process forms the anterior edge of the sockets and has grooves to fit the teeth. The anterior edge of the pad is trilobed, forming half or more of the boundary of the roughly circular adductor muscle scars. The adductor scar area has various secondary ridges, but they are never so well developed as to form trans-muscle septa. Completely anterior of the muscle field there is usually a very fine short median septum. As with the pedicle valve the anterior is very coarsely pustulate, the individual taleolae standing up to 0·5 mm. above the valve floor.

Holotype. B 73340 a complete shell with both valves (figured Reed 1917, pl. 13, fig. 5) from the Middle Llandovery of Woodland Point, Girvan, Ayrshire, Scotland. Gray Collection.

Dimensions (in cm.—all specimens from Woodland Point)

		l_d	w.
B 73340	Holotype, pedicle valve measured	1·32	approx. 3·6
BB 55621	Paratype, pedicle valve .	1·35	2·92
BB 55637	Paratype, pedicle valve .	1·23	2·74
BB 55653	Paratype, pedicle valve .	0·98	2·24
BB 55705	Paratype, brachial valve .	1·18	2·37
BB 55706	Paratype, brachial valve .	1·25	3·60

Discussion. This species is common at the type locality, and seems to have been one of the more successful leptaenids in the Llandovery. It is clearly a direct descendant of its subspecies *L. valentia mullochensis*, described below, which inhabited the same area in the lower Llandovery. Woodland Point is also of interest in that it is one of the localities where both large and small species of *Leptaena* are found side by side, in this case *L. valentia* and *L. reedi*.

Leptaena valentia mullochensis subsp. nov.

(Pl. 8, figs. 9–15)

1917. *Leptaena rhomboidalis* (Wilckens) var. δ Reed : 872, pl. 13, fig. 4.

Holotype. B 73384, a partly exfoliated pedicle valve figured by Reed (1917, pl. 13, fig. 4) from Lower Llandovery beds, Mulloch Hill, Girvan, Ayrshire, Scotland. Gray Collection.

Dimensions (in cm.)		l_d	w.
B 73384	Holotype, pedicle valve	1·44	approx. 3·2
BB 31375	Paratype, pedicle valve	1·24	3·34
BB 73379	Paratype, pedicle valve	0·95	1·92
BB 31386	Paratype, brachial valve	1·28	2·26
BB 31388	Paratype, brachial valve	1·29	1·94

Discussion. This form seems best considered as a subspecies of *L. valentia* as the two are very close in most morphological details, particularly in the internal structures within both valves. There are, however, various minor differences which enables Reed's separation to be confirmed. Rugae counts on pedicle internal moulds give the following results (number of rugae visible up to geniculation).

Rugae Number	*Woodland Point*	*Mulloch Hill*
4	2	0
5	18	3
6	15	8
7	2	5
8	0	2
	n = 37	n = 18

Reed (1917 : 872) noted differences between the two ' varieties ' of the angle at which the rugae meet the hingeline, but this is not supported by the present investigation. The rugae are however, less regular in *L. valentia mullochensis* than in, the typical subspecies, often being interrupted, particularly laterally.

The pedicle valve length of disc/width ratios of the two subspecies are virtually the same, having a mean of 42·8% for Mulloch Hill (n = 21, OR 31·3–57·4) and 41·9% for Woodland Point (n = 53, OR 29·0–52·8). The variability of the pedicle valve muscle field for the whole species is demonstrated by Pl. 8, figs. 10, 12, 13, 14.

Leptaena zeta Lamont

(Pl. 9, figs. 1–6)

1871. *Strophomena rhomboidalis* (Wilckens); Davidson : 281 *pars*, pl. 39, fig. 20 only.
1917. *Leptaena rhomboidalis* (Wilckens) var. ζ Reed : 872, pl. 13, figs. 8, 9.
1947. *Leptaena zeta* Lamont : 200.

Diagnosis. Very large *Leptaena* with mainly parallel-sided muscle area.

Description. *Exterior.* Shape semicircular with variably pronounced alae. Geniculation between 70 and 90 degrees, and trail proportionately shorter than is

usual for the genus. Ornament of subequal parvicostellae and rugae which are usually continuous but are often irregular. Medium-sized interarea with prominent growth lines. Delthyrium mainly closed by large chilidium which appears bilobed as it wraps round the cardinal process lobes. Small foramen plugged by adventitious material.

Pedicle interior. Strong grooved teeth and widely divergent small dental plates, the latter joined to a pair of muscle bounding ridges which flare outward from the valve floor. The ridges are usually subparallel but occasionally curve inwards anteriorly, though never meeting and usually completely open (Pl. 9, figs. 2, 3). Very small median ridge sometimes developed in the muscle area between the small lanceolate adductor scars, themselves inside the strongly impressed diductor scars which often have radiating striae across them. The central area outside the muscle field is coarsely pustulate.

Brachial interior. Strong erect cardinal process lobes very close to the chilidium with faint blade between them. The lobes rest on the posterior end of a strong platform pad, which is often grooved postero-laterally to act as a socket plate. The platform anterior edge is trilobed, surrounding on three sides the pair of prominent subcircular adductor scars. A faint extension of the central platform sometimes extends further anteriorly to become a very small median septum. The central area which merges laterally with the platform is coarsely pustulate.

Lectotype, here designated. B 73355 (the original of Reed 1917, pl. 13, fig. 8), a pedicle exterior from Penkill, Girvan. Gray Collection.

Dimensions (in cm.)			l_d	w.
B 73355	Lectotype, pedicle valve	Penkill	1·97	approx. 4·4
BB 31305	Pedicle valve	Penkill	2·29	approx. 4·7
B 73364	Pedicle valve	Bargany Pond Burn	2·38	approx. 5·8
B 73365	Pedicle valve	Bargany Pond Burn	2·10	approx. 5·2
BB 31469	Pedicle valve	Minsterley Lane	approx. 2·3	6·58
BB 31468	Brachial valve	Minsterley Lane	2·05	3·42

Discussion. This is the largest species of *Leptaena* found in the British Llandovery (though not the largest in the Silurian—this is probably the undescribed species in the Woolhope limestone). It seems confined to the highest beds at Girvan—the Penkill group, and also to the Minsterley Formation of Shropshire. It is not common at any locality.

From the general aspect, particularly the shape of the pedicle and brachial muscle field, it is probably a descendant of *Leptaena valentia* sp. nov. also from the Girvan area.

Leptaena reedi sp. nov.

(Pl. 10, figs. 1–14)

1917. *Leptaena rhomboidalis* (Wilckens) var. *ε* (young shell) Reed : 872, pl. 13, fig. 7.

Diagnosis. Small *Leptaena*, transverse, thick shelled, with large area and pseudodeltidium.

Description. *Exterior.* Shape transverse with large alae, sometimes quadrate anteriorly. Geniculation often more than 90 degrees with the trail sometimes bending back under the disc. Ornament of subequal parvicostellae, coarser on the disc than on the trail. Symmetrical rugae on the disc, but no trace on the trail. Large interarea, particularly in the pedicle valve. Delthyrium closed partly by pseudodeltidium, partly by chilidium. Small supra-apical foramen plugged in most specimens.

Pedicle interior. Strong grooved teeth attached to a pair of distinct bilobed muscle bounding ridges which sometimes meet anteriorly, but which are sometimes divided by a small median septum. Diamond shaped adductor scars on a ridge raised between the triangular diductor scars, which are sometimes grooved. Coarse taleolae on the disc outside the muscle field. Thick shell.

Brachial interior. Erect, posteriorly directed bilobed cardinal process. Raised platform with variably developed trans-muscle septa. Short median septum sometimes developed but often absent in the muscle field. Interior reflection of rugae but not ornament. Sharp geniculation usually present, inside which is a well developed taleolae field.

Holotype. B 73341, a complete shell (figured by Reed 1917, pl. 13, fig. 7) from Woodland Point, Girvan, Ayrshire. Gray Collection.

Dimensions (in cm.)		l_d	w.
B 73341	Holotype, pedicle valve	0·51	approx. 1·5
BB 31457	Paratype, pedicle valve	0·75	1·72
BB 31461	Paratype, brachial valve	0·68	1·81
B 73342	Paratype, brachial valve	0·66	1·38

Discussion. Reed mistook this species for the young of *L. valentia* and they occur mixed intimately (e.g. Pl. 10, fig. 10) but the two are clearly distinct in nearly every feature.

L. reedi is rare at the type locality, although the Gray Collection contains about thirty specimens, and has not been found elsewhere than at Woodland Point. Its affinities are uncertain. No other species of *Leptaena* resembles it, and the large interarea is unique amongst Silurian strophomenids. The brachial muscle field is more reminiscent of *Cyphomena* or some of the strophomenids than of other species of *Leptaena*.

Leptaena ziegleri sp. nov.

(Pl. 11, figs. 1–5)

Diagnosis. Small *Leptaena* with oval pedicle muscle field, and possessing strong socket plates.

Description. *Exterior.* Shape semicircular, occasionally quadrate with small alae. Geniculation usually at right angles. Ornament of faint subequal parvicostellae, rugae symmetrical and numerous but faint. Interarea small. Delthyrium probably mainly open, but no information on possible chilidium. Foramen not seen.

Pedicle interior. Prominent teeth and dental plates joined to strong muscle bounding ridges. The latter are of oval, almost circular shape, but not quite meeting anteriorly. Adductor scars are not seen, diductor scars are poorly impressed within the muscle bounding ridges. Faint median septum in one specimen only (OUM C4147) otherwise absent.

Brachial interior. Small, erect, bilobed cardinal process ankylosed to strong pair of socket plates. Brachial muscle field not impressed and details of muscalature not known. Very faint trace of median septum seen in some specimens only. Raised rim at edge of disc.

Holotype. OUM C4146, a pedicle valve internal mould from the Wych Beds (Upper Llandovery), Malvern Hills, Herefordshire. Grid Ref. SO/7612 3811.

Dimensions (in cm.)	l_d	w.
OUM C4146 Holotype, pedicle valve .	0·64	1·05
OUM C4147 Paratype, pedicle valve .	0·54	1·25
OUM C4137 Paratype, brachial valve .	0·58	approx. 1·9
OUM C4136 Paratype, brachial valve .	0·64	approx. 1·4

Discussion. The species is known only from its type locality. It is distinctive in pedicle and brachial internal structures and in its shape and ornament. The species is named after Dr. A. M. Ziegler, who collected the material.

Leptaena quadrata Bancroft

(Pl. 11, figs. 6–10)

1949. *Leptaena quadrata* (Reed MS) Bancroft 1949 : 7, pl. 1, figs. 28–30.

Diagnosis. Small quadrate *Leptaena* with many fine rugae.

Description. *Exterior.* Shape quadrate with small but pronounced alae. Small trail after geniculation of approximately 80 degrees. Ornament of fine symmetrical rugae and faint subequal parvicostellae. Interarea of average size. No information on possible pseudodeltidium; small chilidium present. Foramen not known, but probably small.

Pedicle interior. Small divergent teeth joined to variably developed muscle bounding ridges. The latter are long and sub-parallel, sometimes merging anteriorly with the valve floor (Pl. 11, fig. 6), sometimes swinging round in an irregularly bilobed fashion (Pl. 11, fig. 10). A pair of elongate adductor scars between the impressed long diductor scars. Median septum absent.

Brachial interior. Erect bilobed cardinal process. Weak platform posteriorly acting as socket plates, anteriorly enclosing weakly impressed adductor muscle field of approximately oval shape. Sometimes very thin median septum weakly developed.

Lectotype, here selected. SMA 32437 a pedicle valve internal and external mould (figured Bancroft 1949, pl. 1, fig. 28) from Uzmaston Beds (Upper Llandovery),

O. T. Jones Collection, ' locality K, below path south west of Uzmaston,' The Frolic, near Haverfordwest, Pembrokeshire.

Dimensions (in cm.)		l_d	w.
SMA 32437	Lectotype, pedicle valve .	0·73	0·86
SMA 32444	Pedicle valve . . .	0·55	0·86
SMA 32438	Brachial valve . . .	0·63	1·02
SMA 32441	Brachial valve . . .	0·53	0·93

Discussion. This species is known only from its type locality where it occurs in a slightly crushed greenish siltstone. Its associates are *Amphistophia whittardi* Cocks, *Pentlandina parva* Bancroft, *Dicoelosia* cf. *alticavatus* (Whittard & Barker), *Coolinia* sp., *Atrypa* sp., *Eospirifer* sp. and *Eoplectodonta millinensis* (Jones), which indicate on balance a *Clorinda* community, although no pentamerids have been seen.

The usual leptaenid in the Welsh Borderland *Clorinda* community is *L. purpurea* sp. nov., and Bancroft's species may be related to it. *L. purpurea* has, however, a completely different muscle field disposition in both pedicle and brachial valves, and different overall proportions. It is also larger.

Leptaena purpurea sp. nov.

(Pl. 12, figs. 1–6)

1932. *Leptaena* sp. nov. Whittard, table facing p. 896.

Diagnosis. Small quadrate *Leptaena* with usually oval-sided pedicle muscle bounding ridges.

Description. *Exterior.* Shape quadrate with small ears. Sharply geniculate with approximately a right angle between disc and trail, but the angle varies between obtuse and acute. Ornament of fine, subequal parvicostellae, with new costellae arising by intercalation. Rugae cover the whole disc on both valves; they are fairly regular and have a small wavelength. Small external rim on the ventral knee and a small groove on the dorsal knee. Open delthyrium, large chilidium, but rather smaller interarea than is common for the genus. No information on the pedicle foramen, except of a very young specimen (OUM C13141) in which it is supra-apical and probably, at that stage, functional.

Pedicle interior. Straight hingeline with open delthyrium flanked by relatively large dental plates, considering the small size of the species which are combined in part with a raised posterior extension of the muscle bounding ridges. Faint muscle grooves often seen on the muscle field. Diductor scars bilobed and surrounded laterally by pronounced bounding ridges which in some specimens curve round anteriorly to form an ω shape, although they do not quite meet in the centre. Small lanceolate adductor scars, though seldom seen, are separated by a fine median ridge which in a few specimens continues anteriorly of the muscle bounding ridges. In completely preserved specimens there is a ridge running about half-way down the trail and nearly all the way round it, but postero-laterally crossing the geniculation and merging at a low angle with the hingeline, although on many specimens the ridge is very faint. Pseudopunctae coarse near the umbo, except where absent in the

muscle field. They are apparently randomly distributed near the umbo, but antero-laterally they tend to be arranged in lines parallel to both the rugae and the ornament.

Brachial interior. Raised cardinal process with two stout lobes directed ventrally. Large chilidium fused close to the base of the cardinal process. Anchor shaped platform present, the haft of which forms a median ridge dividing the two pairs of oval adductor muscle scars, which are separated from each other by the pair of low short ridges running laterally from each side of the haft. Disc surrounded by raised rim, which is reflected to a lesser extent by the exterior groove, indicating a local thickening of the shell material. Mantle canals visible occasionally (Pl. 12, fig. 3) coming from the floor of the disc, up over the rim and fading towards the valve margin. No bifurcations seen. Pseudopunctae very noticeable postero-medianly, but scarcely visible on rim or trail.

Holotype. BB 31465, a pedicle internal mould from the Purple Shale (Upper Llandovery) of Domas, Shropshire. Grid Ref. SJ/5936 0062.

Dimensions (in cm.).			l_d	w.
BB 31465	Holotype, pedicle interior	Domas	0·52	1·06
BB 31466	Paratype, brachial interior	Hughley	0·51	1·19
OUM C12062	Paratype, pedicle interior	Onny River	0·54	1·08
OUM C13480	Paratype, brachial exterior	Domas	0·43	1·15
OUM C13478	Paratype, brachial exterior	Domas	0·47	1·21
OUM C13477	Paratype, brachial exterior	Domas	0·45	1·20
OUM C13482	Paratype, pedicle interior	Domas	0·41	0·79
OUM C13141	Paratype, brachial exterior	Wall-under-Heywood	0·20	0·29

Discussion. Although leptaenids are to be found in nearly every collection from the Purple Shales, they are never common, but those that do occur are usually attributable to this form. The species is small, and thus only strictly comparable with *L. quadrata* Bancroft from the Upper Llandovery of the Frolic, Haverfordwest, from which it differs in its larger teeth, encircling muscle ridges and the character and strength of the rugae.

One specimen of a leptaenid of comparable size, 1·35 cm. wide, has been collected (Bristol University Museum 12101) from the contemporary Damery Beds (C_5) of Tortworth by Dr. M. L. K. Curtis. The specimen, a pedicle valve (Pl. 12, fig. 6), differs from *L. purpurea* in the indented shape of the muscle bounding ridges and also in the almost complete absence of internal ornament or rugae, but in general shape and size it is similar. Without further material, particularly brachial valves, any definite attribution seems unwarranted.

Leptaena sp.

(Pl. 12, figs. 7, 8)

Exterior description. Shape quadrate and alate. Ornament of subequal, fine parvicostellae. Small rugae, uneven round the disc, but giving the illusion of not

being so. At least eighteen rugae of subequal wavelength (except near the umbo) on the ventral disc and sixteen on the dorsal. Geniculation less than right angles on the ventral valve, but the trail curves into a steeper angle, meeting the anterior margin at an acute angle with the disc. Small external rim on the ventral knee, and small external groove on the dorsal knee. Prominent interarea. Open delthyrium, large chilidium, with growth-lines persisting to the interarea. Small foramen about 0·2 mm. diameter.

Locality. Purple Shales, ' near Harley ', Shropshire.

Dimensions. width = 3·6 cm. approx., length = 1·73 cm., length of disc = 1·43 cm., height of trail = 1·2 cm.

Discussion. In the late Professor Whittard's collection there is one complete specimen (BB 31467) of *Leptaena* which cannot be assigned with confidence to any described species, but until interior details are known, to name a new species would be premature. Though too big for *Leptaena purpurea* it is sufficiently close to it for the possibility of a sport not to be ruled out completely, despite its large disc and overall size. Its shell thickness, interarea, and general proportions are much finer and more delicate than the Wenlock *L. depressa*. It may, however, be related to a large, undescribed species of *Leptaena* present in the Woolhope Limestone of Crickley Common, Herefordshire and elsewhere.

Genus ***CYPHOMENA*** Cooper 1956

Type species. *Leptaena homostriata* Butts 1942 from the Oranda Formation (Middle Ordovician) of Virginia, North America.

Discussion. When Cooper (1956 : 840) erected *Cyphomena* he put into it three species (and tentatively a fourth), all from the Middle Ordovician of North America. Subsequently Williams (1962 : 203) recognized one of them in the Scottish Caradocian. These are the only published records.

The interior disposition and external form of the various species of *Cyphomena*, so well figured by Cooper, leave no doubt of the close relationship between them and some species present in the Llandovery. In particular the gradually curving pedicle valve and sharply geniculate brachial valve, the proportions and disposition of the musculature and denticulation in both valves, and the small curved pseudodeltidium not completely filling the delthyrium, above which is developed a sufficiently large pedicle foramen for it to be considered functional, are identical in Ordovician and Silurian specimens.

There is, however, one point of difference in that Cooper's genus ' never developed the concentric wrinkling of the visceral region ' (1956 : 841). It is true that complete rugae of the type found in *Leptaena* are not seen in the Silurian forms, but interrupted, sometimes zig-zag, rugae between the costellae are often well-developed, for example in *C. wisgoriensis*. This is in contrast to the simple costellae of the Caradocian species. This zig-zag type of ornament occurs many times in the Strophomenida and must be polyphyletic, perhaps the best-known example being the plectambonitacean *Ptychoglyptus*. In addition there occurs in the Llandovery a form, described

below, which apparently lacks ornament of any kind, but has interior and general form very close to the Ordovician species.

Thus to satisfactorily represent the close relationship between all these forms, but also to bring out their inherent differences, two new subgenera of *Cyphomena* are proposed here, one, *Cyphomenoidea*, to include forms with interrupted rugae, and the other, *Laevicyphomena*, to include forms, only one of which is at present known, which lack exterior ornament of any kind.

CYPHOMENA (CYPHOMENOIDEA) subgen. nov.

Diagnosis. *Cyphomena* with parvicostellate ornament, the major ribs interrupting small, irregular rugae over the whole shell.

Type species. *Leptaena wisgoriensis* Lamont & Gilbert 1945.

Range. Llandovery, ?Wenlock Series.

Discussion. The same type of ornament as appears on *Cyphomenoidea* may also be seen on many species of *Pentlandina*, for example the contemporaneous *Pentlandina loveni* (de Verneuil 1848) from the Visby Marl of Gotland. It is seen again on *Strophomena julia* Billings 1862 from the Jupiter Formation (Upper Llandovery) of Anticosti Island, Canada, but in this case illustrations of the interior are not available. A topotype in the British Museum (B 76891), a complete shell with both valves joined, has the correct profile for the new subgenus, but the species may be a strophomeninid and cannot be referred to *Cyphomenoidea* with confidence until the interior is known.

Cyphomena (Cyphomenoidea) wisgoriensis (Lamont & Gilbert)

(Pl. 12, figs. 9–12)

1945. *Leptaena wisgoriensis* Lamont & Gilbert : 660, pl. 3, figs. 10–14.
1951. *Leptaena wisgoriensis* Williams : 119.

Type locality. Sunken track through Coneygore Coppice, near Alfrick, Worcestershire [Grid Ref. SO/7464 5111].

Discussion. A full description of the species may be found in Lamont & Gilbert (1945 : 660–662). Although a large collection in the Oxford University Museum by Dr. Ziegler from the type locality failed to produce specimens of *C. wisgoriensis*, good material was found at Grid Ref. SO/7430 5152, less than a third of a mile away and at the same stratigraphical horizon, and some is illustrated here. A comparison of Pl. 12, fig. 10 with pl. 224, fig. 21 of Cooper (1956) reveals that the interior of the brachial valves of *C. wisgoriensis* and *C. angulata* Cooper are virtually identical, apart from the smaller size, more pronounced reflection of the ribbing (or possibly pallial sinuses) and slightly larger anterior median ridge of the latter species. In particular the distinctive shape of Cooper's species, with a sharp geniculation and raised rim in the brachial valve and much more gentle curve without geniculation in the pedicle valve, together with the close similarity of internal structures in both valves, pronounce them to be close relatives.

The major difference between the two lies in the nature of the ornament, as mentioned in the discussion of the genus. All three species described by Cooper have more or less equally costellate ornament, whereas *C. wisgoriensis* has a subequal parvicostellate ornament, upon which is superimposed small irregular rugae separated from each other by the larger ribs, forming a regular zig-zag pattern (Pl. 12, fig. 12).

The species has been recognized only from the Wych Beds (C_{5-6} in age) of the North Malverns and Ankerdine Hill, but a solitary external mould of a brachial valve from the Purple Shale of Hughley, Shropshire, has a similar ornament and may tentatively be referred to *C. wisgoriensis*.

CYPHOMENA (LAEVICYPHOMENA) subgen. nov.

Diagnosis. *Cyphomena* with no shell ornament.

Type species. *Cyphomena* (*Laevicyphomena*) *feliciter* sp. nov.

Range. Middle to Upper Llandovery Series.

Discussion. The new subgenus has as yet only one species attributed to it. Although it is fairly certain that the latter has no ornament, it has admittedly been found so far only in sandstone matrices, and it is possible that some sort of very fine ornament might have escaped detection.

Cyphomena (Laevicyphomena) feliciter sp. nov.

(Pl. 12, figs. 13–14, Pl. 13, figs. 1–9)

1932. *Stropheodonta funiculata* (M'Coy); Whittard *pars*, table facing p. 896.

Diagnosis. Smooth *Cyphomena* with laterally concave ridges in the brachial valve.

Description. *Exterior.* Shape trapezoidal, varying sometimes to semicircular, particularly in the outline of the brachial geniculation. Sometimes slightly alate. Pedicle valve has a gradual convexity, always less than a total of 90 degrees, but brachial valve flat apart from its geniculation. No visible ornament, but fine growth-lines have been observed on the trail only of a few specimens, and the shell surface may be slightly buckled (rugate would be too definite a term) near the lateral extremities only. Interarea medium-sized to small for a leptaenid. Small chilidium. Functional foramen at apex of pedicle valve, below which is a small pseudodeltidium apparently not entirely covering the delthyrium.

Pedicle interior. Thickened hinge line, the anterior edge of which diverges laterally away from the umbo until it reaches the edge of the trail, where it thins and becomes flush with the main shell. Prominent dental plates (but short in a dorsal direction) diverge at an angle of 90 degrees or more, and continue anteriorly as muscle bounding ridges which persist for a short distance in the same direction, but then swing through an angle of 60–80 degrees to converge again, though they do not meet. Thus the pedicle muscle field is somewhat similar to that of a strophomeninid, except when the species becomes gerontic (Pl. 13, fig. 7), and an anterior fold connects

the two bounding ridges, overriding the median septum which in young specimens divides them. Rarely (e.g. Pl. 13, fig. 1) the muscle field presents a rather more bilobed appearance, with the median septum poorly developed except anteriorly. No trace of pseudopunctae seen.

Brachial interior. Straight hinge line, to which is fused a pair of widely divergent socket plates. Two small cardinal process lobes approximately at right angles to the valve floor. Small platform, ending anteriorly with a very short, small median ridge, a trace of which may often be seen again in the anterior part of the disc, although it is never continuous. From approximately the antero-lateral end of the socket plates, and usually separated from them by a short gap, run a pair of ridges, subparallel to the median plane but concave outwards. The degree of concavity varies, and a small proportion are almost straight. These ridges bound the anterior pair of adductor muscle scars, which are particularly elongate. The posterior pair are smaller, approximately round, and situated immediately anterior of the socket plates. They are occasionally separated from the anterior adductors by two poorly-developed small nodes, which are just posterior of the point of closest proximity of the two bounding ridges. The geniculation is sharp (in contrast to the pedicle valve) and often associated with a marked interior rim, which is not reflected on the exterior. No trace of pseudopunctae observed.

Holotype. BB 31346, a pedicle valve from the Bog Quartzite of Bog Mine, Shropshire [Grid Ref. SO/3510 9815]. Other localities (all in Shropshire): Napp Outlier [SO/3493 9922], Josey's Wood [SJ/3653 0221] and Bank Outlier [SJ/3821 0418].

Dimensions (in cm.)			l	w.
BB 31346	Holotype, pedicle valve	Bog	0·62	1·45
BB 31345	Paratype, pedical valve	Bog	0·74	2·02
OUM C9895	Paratype, pedicle valve	Bog	0·70	1·40
OUM C10988	Paratype, pedicle valve	Josey's Wood	0·78	1·52
BB 31348	Paratype, brachial valve	Bog	0·71	1·96
OUM C9893	Paratype, brachial valve	Bog	0·68	—
BB 31347	Paratype, brachial valve	Bog	0·69	1·61
BB 31352	Paratype, brachial valve	Napp Outlier	0·71	1·71

Discussion. It is unfortunate that this distinctive species should be preserved only in fairly coarse matrices, so that fine details of possible ornament or arrangement of pseudopunctae cannot be observed. So far the species is confined to the Bog Quartzite and Venusbank Formation of Shropshire; only two specimens (OUM C10988 from Josey's Wood and BB 31354 from Bank Outlier) have been recovered from the latter horizon, and the species does not occur above 1% in any collection.

C. feliciter is not far removed from *C. wisgoriensis* and other older species of *Cyphomena*, but differs from them in many ways—the lack of distinctive ornament, the development of the brachial ridges, and the general proportions and shape of the valves. However there are sufficient characteristics in common, particularly the general internal arrangement, the open foramen and small pseudodeltidium,

and the geniculation angles in both valves, to enable the new species to be included in *Cyphomena* with a fair degree of confidence.

Genus *MACKERROVIA* nov.

Diagnosis. Irregularly geniculate leptaenid with long diductor scars in the pedicle valve, bounded laterally by high irregular ridges, and partially mirrored in the brachial valve by long anterior adductor scars, bounded by less pronounced ridges. Shell surface often irregular. Very faint, often invisible ornament of differentiated parvicostellae. Pedicle atrophied in adults.

Type species. *Brachyprion arenaceus* var. *lobatus* Lamont & Gilbert 1945 emended below, the only known species.

Discussion. *Mackerrovia* is quite different from any genus yet described, and its attribution to the leptaeninids rather than to any other subfamily within the Strophomenidae is based mainly upon the geniculation. The most distinctive feature is the long muscle scars bounded by high ridges in the pedicle valve (and corresponding traces in the brachial valve). This is paralleled only by a homoeomorphic development in the Strophеodontidae, namely *Shaleria* and to a lesser extent some species of *Amphistrophia*, but in these genera the ridges are much more uniform. The present genus is not a strophеodontid, despite its previous ascription to *Brachyprion*, and the whole internal structure is quite different, in addition to there being no trace of denticles on the hingeline. As well as possessing the long scars, *Mackerrovia* differs from other leptaeninid and strophomeninid genera in the usual absence of rugae and also the highly irregular shell surface, which is more reminiscent of some Upper Palaeozoic davidsoniaceans.

The genus, known so far only from the higher part of the Upper Llandovery in the Welsh Borderland, is named after Dr. W. S. McKerrow.

Mackerrovia lobatus (Lamont & Gilbert)

(Pl. 13, figs. 10–15; Pl. 14, figs. 1–8)

1871. *Strophomena arenacea* [Salter MS] Davidson *pars*, pl. XLII, figs. 7–8, *non* fig. 6.
1945. *Brachyprion arenaceus* var. *lobatus* Lamont & Gilbert : 667, pl. VI, fig. 6, pl. VII, fig. 2.
1945. *Brachyprion arenaceus* var. *geniculatus* Lamont & Gilbert : 669, pl. VI, figs. 1–5, pl. VII, fig. 3.
1953*a*. *Brachyprion arenaceus* var. *geniculatus* Lamont & Gilbert; Williams : 23.

Diagnosis. As for genus.

Description. *Exterior.* Shell shield-shaped with no alae. More or less sharp geniculation occurs at a variable length (occasionally, e.g. Pl. 13, fig. 15, two geniculations are visible). Shell surface uneven and irregular in detail. Some specimens show well-developed growth lines. Ornament of extremely faint parvicostellae with even smaller stripes between them, but this is not seen on most specimens. Hingeline straight, but immediately anterior to it the shell often curves up (viewed from the posterior) from the umbo. Pseudodeltidium closes the delthyrium flush

with the interarea, the latter being of variable size and sometimes scarcely developed at all in the brachial valve. No trace of a foramen observed.

Pedicle interior. Thickened hingeline with medium-sized teeth that protrude anteriorly as well as ventrally. Long diductor muscle scars are of irregular shape and enclose long adductor scars separated by a small but persistent median ridge. Round the scars, posteriorly as an extension of the teeth, are long, high bounding ridges of variable shape, subparallel, concave or convex, or a mixture of the three. Sometimes they converge anteriorly (Pl. 14, fig.1), sometimes they diverge (Pl. 14, fig. 7). They usually double back round the anterior end of the diductors, but are always prevented from meeting by the median ridge. Usually the bounding ridges are not at right angles to the valve floor, but are directed dorso-laterally. The whole muscle area is not always in the median plane, and may be directed anteriorly either to right or left. Fairly large pseudopunctae visible on most specimens everywhere except on the muscle field.

Brachial interior. Prominent cardinal process lobes directed ventrally, but diverge anteriorly. Long narrow sockets diverge at just over 90 degrees, bounded anteriorly by slender socket plates whose posterior half lies latero-posteriorly, and very close, to the cardinal process lobes. The socket is bounded posteriorly by a slight elevation of the hingeline. Very weak platform ends anteriorly in a broad, weak median ridge dividing the posterior pair of adductor muscle scars. The ridge bifurcates and then closes together again, leaving a faint pit (Pl. 14, fig. 5), after which it becomes narrow but more pronounced, dividing the anterior adductors and continuing, in some cases, nearly to the edge of the disc. No muscle bounding ridges near the umbo, but about a third of the way to the trail they suddenly appear, to persist strongly anteriorly for 5–10 mm., though never so pronounced as in the pedicle valve. Fairly large pseudopunctae visible everywhere except in the muscle field.

Lectotype, here selected. GSM 11461, a pedicle valve from Wych Beds (Upper Llandovery), Gunwick Mill, Malvern Hills, Worcestershire.

Dimensions (in cm.).		l	w.
Bristol 12143	Pedicle valve	2·00	1·57
Bristol 12144	Pedicle valve	1·93	2·46
Bristol 12159	Pedicle valve	2·42	approx. 2·7
Bristol 12180	Pedicle valve	2·42	3·08
Bristol T.1	Pedicle valve	2·19	approx. 2·5
OUM C652	Tortworth pedicle valve . .	2·08	1·92
OUM C654	' May Hill sst.' pedicle valve .	2·59	approx. 2·7
OUM C5649	H-M-B pedicle valve . .	1·72	2·01
OUM C5641	H-M-B brachial valve length of trail . . .	1·16	approx. 1·1

The widths quoted are those of the hingeline, which is by no means always the widest part of the valve.

Discussion. Lamont & Gilbert did not fully describe their varieties, but gave good illustrations of the pedicle valves (although no brachial valves were shown),

and there is no doubt of the shells they had in mind, which are the same as that figured by Davidson (1871, pl. XLII, figs. 7, 8). The systematic situation surrounding this species and *Brachyprion arenacea* has been discussed elsewhere (Cocks 1967 : 257).

Lamont & Gilbert's two ' varieties ' are considered to be one homogeneous species, although this shows a remarkable range of variation in many details. They (1945) enumerated two differences between the varieties: (i) *lobatus* was more or less evenly curved, whereas *geniculatus* was geniculate, (ii) they had found no specimens of *lobatus* with concave muscle boundary ridges, although they admitted that convex forms were to be seen in both varieties. In fact a collection from Gunwick Mill shows all variations of geniculation in a single rock band, and a specimen from collection T-R-A, OUM C3690/1, shows a *lobatus* (*sensu* Lamont & Gilbert) shell shape with concave ridges.

Lamont & Gilbert (1945, p. 668) selected two syntypes, BU 397 and GSM 11461. As the first comes from 1030 feet down the Cooperative Society's borehole at Walsall, I propose to select the second specimen as lectotype. This is also the first specimen figured by Davidson (1871, pl. XLII, fig. 7) and comes from Gunwick Mill [Grid Ref. SO/7430 5152], a locality in which the species occurs up to 5% and may be procured easily today. In addition the Birmingham specimen is poorly preserved and incomplete, whereas the lectotype is well preserved and shows the typical musculature.

The species is not common (never more than 5%) at any locality, but has been found in the top part of the Upper Llandovery in beds of C_5 and C_6 age at Tortworth, May Hill, the Malverns, Ankerdine Hill, Shropshire, Rubery and Walsall, but has not so far been recovered outside the Welsh Borderland.

BELLIMURINA Cooper, 1956

Bellimurina sp.

(Pl. 14, figs. 9, 10)

A single specimen in the British Museum, B 8490, not accurately localized, but from 'Deerhope, Pentland Hills, Scotland,' may be referred to *Bellimurina*, a genus not so far recorded apart from Cooper's original description (1956) from the Middle Ordovician of America, and a record in the Caradocian of Girvan (Williams 1962). The specimen is a natural mould of an exterior of a brachial valve, and the attached cardinal area of a pedicle valve. Also on the same slab is a specimen of *Eoplectodonta* which confirms the late Llandovery age of the specimen. The ornament of the leptaeninid is typical of *Bellimurina*; differentiated parvicostellae, the larger of which separate the pattern of broken rugae. The shell is much larger (length 1·83 cm.) than contemporary *Cyphomenoidea*, which has a similar ornament, and the irregular shell shape and rough geniculation with the frilly lamellae on the gerontic trail have not been found in the latter subgenus.

Thus the stratigraphical range of *Bellimurina* is significantly increased.

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IV. REFERENCES

Amsden, T. W. 1949. Stratigraphy and paleontology of the Brownsport Formation (Silurian) of Western Tennessee. *Bull. Peabody Mus. Nat. Hist.*, New Haven, **5** : 1–138, pls. 1–34.

—— 1951. Brachiopods of the Henryhouse Formation (Silurian) of Oklahoma. *J. Paleont.* Tulsa, **25** : 69–96, pls. 15–20.

Bancroft, B. B. 1949. *Welsh Valentian Brachiopods and the* Strophomena antiquata *group of fossil brachiopods.* 15 pp., 3 pls., privately printed. Mexborough.

Barrande, J. 1848. *Über die Brachiopoden der Silurischen Schichten von Boehmen.* part 2. 104 pp., pls. 16–23. Vienna.

—— 1879. *Système silurien du centre de la Bohême.* lère partie; volume V. Classe des Mollusques. Ordre des Brachiopodes. 226 pp., 153 pls. Prague & Paris.

Boucot, A. J., Johnson, J. G., Harper, C. W. & Walmsley, V. G. 1966. Silurian brachiopods and gastropods of Southern New Brunswick. *Bull. geol. Surv. Can.*, Ottawa, **140**: 1–145, pls. 1–18.

Chernychev, B. B. 1937. The Silurian brachiopods of Mongolia and Tuva (in Russian and English). *Trudy Mongolian Comm.*, **29**. *Izdatelstvo, Akad. sci. USSR.*, Moscow, 1–94, pls. 1–5.

Cocks, L. R. M. 1967. Llandovery stropheodontids from the Welsh Borderland. *Palaeontology*, London, **10** : 245–265, pls. 37–39.

—— 1967*a*. Depth patterns in Silurian marine communities. *Marine Geol.*, Amsterdam, **5**: 379–82.

Cooper, G. A. 1956. Chazyan and related brachiopods. *Smithson. Misc. Coll.*, Washington, **127** : 1–1245, pls. 1–269.

Dalman, J. W. 1828. Uppstallning och Beskrivning af de i sverige funne Terebratuliter. *K. Svenska Vetensk. Akad. Hand.*, Stockholm, for 1827 : 85–155, pls. 1–6.

Davidson, T. 1847. Observations on some of the Wenlock-limestone Brachiopoda, with descriptions of several new species. *Lond. geol. Jl.*, **1** : 52–65, pls. 12, 13.

—— 1848. Mémoire sur les Brachiopodes du système silurien supérieur d'Angleterre. *Bull. Soc. géol. Fr.*, Paris, (2) **5** : 309–338, pl. 3.

—— 1868. On the Upper Silurian Brachiopoda of the Pentland Hills, and of Lesmahagow, in Lanarkshire. *Trans. geol. Soc. Glasgow* (Pal. Ser.) **1** : 1–24, pls. 1–3.

—— 1871. British fossil Brachiopoda, 3, Part 7, no. 4, Silurian. *Palaeontogr. Soc.* [*Monogr.*], London, **24** : 249–397, pls. 38–50.

—— 1883. Supplement to the fossil Brachiopoda, 5, Part 2, (Silurian). *Palaeontogr. Soc.* [*Monogr.*], London, **37** : 135–142, pls. 8–17.

FOERSTE, A. F. 1909. Preliminary notes on Cincinnatian fossils. *Bull. sci. labs Denison Univ.* **14** : 209–228, pl. 4.

GAGEL, C. 1890. Die Brachiopoden der Cambrischen und Silurischen Geschiebe im Diluvium der Provinzen Ost-und Westpreussen. *Beitr. Naturk. Preuss*, Konigsberg, **6** : 1–79, pls. 1–5.

HALL, J. & CLARKE, J. M. 1894. *An introduction to the study of the Genera of Palaeozoic Brachiopoda.* Part 2. Palaeontology of New York 8 : (xvi) 1–394, pls. 21–84. Albany.

HAVLÍČEK, V. 1963. Familie Leptaenidae (Brachiopoda) im Böhmischen Altpaläozoikum. *Cas. Národního Muz. Odd.*, Prague, **82** : 220–225, pls. 1, 2.

—— 1968. Brachiopoda of the suborder Strophomenida in Czechoslovakia. *Rozpr. Ústr. Úst. Geol.*, Praha, **33** : 1–225, pls. 1–52.

IMBRIE, J. 1956. Biometrical methods in the study of invertebrate fossils. *Bull. Am. Mus. nat. Hist.*, Washington, **108** : 211–246.

KINDLE, E. M. 1915. Notes on the geology and palaeontology of the Lower Saskatchewan River Valley. *Bull. geol. Surv. Can. Mus.*, Ottawa, **21** : 1–25, pls. 1–4.

LAMONT, A. 1947. Gala-Tarannon Beds in the Pentland Hills, near Edinburgh. *Geol. Mag., Lond.*, **84** : 193–208, 289–303.

—— & GILBERT, D. L. F. 1945. Upper Llandovery Brachiopoda from Coneygore Coppice and Old Storridge Common, near Alfrick, Worcestershire. *Ann. Mag. nat. Hist.*, London, ser. 11, **12** : 641–682, pls. 3–7.

LINDSTRÖM, G. 1860. Bidrag till kännedomen om Gotlands Brachiopoder. *Öfvers. K. Vetens. Akad. Förh.*, Stockholm, **17** : 337–382, pls. 12, 13.

MITCHELL, G. H. & MYKURA, W. 1962. The geology of the neighbourhood of Edinburgh. *Mem. geol. Surv. U.K.*, London, **32** : 1–159, pls. 1–4.

MURCHISON, R. I. 1839. *The Silurian system founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford; with descriptions of the coal fields and overlying formations.* 768 pp., pls. 1–37. London.

NIKIFOROVA, O. I. & ANDREEVA, O. N. 1961. Stratigraphy of the Ordovician and Silurian of the Siberian Platform and its palaeontological basis. (Brachiopods). *Biostratigraphiya Palaeozoya Sibirskov Platformy*, Leningrad, **1** : 1–412, pls. 1–56.

REED, F. R. C. 1917. The Ordovician and Silurian Brachiopoda of the Girvan district. *Trans. roy. Soc. Edinb.*, **51** : 795–998, pls. 18–22.

SHALER, N. S. 1865. List of the Brachiopoda from the island of Anticosti sent by the Museum of Comparative Zoology to different institutions in exchange for other specimens, with annotations. *Bull. Mus. comp. Zool. Harv.*, Cambridge, **1** : 61–70.

SOKOLSKAYA, A. N. 1954. Strophomenids of the Russian Platform (in Russian). *Trudy palaeont. Inst.*, Moscow, **51** : 1–191, pls. 1–18.

—— 1960. Order Strophomenida. *In Osnovy Palaeontologii*; Mshanki, brakhiopody, vol. ed. T. G. SARYCHEVA, Moscow : 1–324, pls. 1–75.

SOWERBY, J. de C. 1823–25. *The Mineral Conchology of Great Britain*, **5** : 171 pp., pls. 408–503. London.

SPJELDNAES, N. 1957. The middle Ordovician of the Oslo Region, Norway. 8. Brachiopods of the Suborder Strophomenida. *Norsk geol. Tidsskr.*, Bergen, **37** : 1–214, pls. 1–14.

TWENHOFEL, W. H. 1928. Geology of Anticosti Island. *Mem. geol. Surv. Brch Can.*, Ottawa, **154** : 1–481, pls. 1–60.

VERNEUIL, P. E. P. de, 1848. Note sur quelques Brachiopodes de l'île de Gothland. *Bull. Soc. géol. Fr.*, Paris, (2) **5** : 339–353, pl. 4.

WAHLENBERG, G. 1821. Petrificata Telluris Svecanae examinata. *Nova Acta R. Soc. Scient. Upsal.*, **8** : 1–116, pls. 1–7 (for 1819).

WHITTARD, W. F. 1932. The stratigraphy of the Valentian rocks of Shropshire. The Longmynd-Shelve and Breidden outcrops. *Q. Jl geol. Soc. Lond.*, **87** : 859–902, pls. 58–62.

WILLIAMS, A. 1951. Llandovery brachiopods from Wales with special reference to the Llandovery district. *Q. Jl geol. Soc. Lond.*, **107** : 85–136, pls. 3–8.

—— 1953. The classification of the strophomenoid brachiopods. *J. Wash. Acad. Sci.*, **43** : 1–13.

—— 1953*a*. North American and European stropheodontids: their morphology and systematics. *Mem. geol. Soc. Am.*, New York, **56** : 1–67, pls. 1–12.

—— 1962. The stratigraphy and brachiopod faunas of the Barr and Lower Ardmillan Series (Caradoc) of the Girvan district of S.W. Ayrshire. *Mem. geol. Soc. Lond.*, **3** : 1–267, pls. 1–25.

—— 1963. The Caradocian brachiopod faunas of the Bala District, Merionethshire. *Bull. Br. Mus. nat. Hist. (Geol.)*, London, **8**: 329–471, pls. 1–16.

—— *et al.* 1965. *Treatise on Invertebrate Paleontology, Part H, Brachiopoda.* Ed. R. C. Moore, Univ. Kansas and Geol. Soc. Am.: 1–297, figs. 1–746.

Ziegler, A. M. 1965. Silurian marine communities and their environmental significance. *Nature, London,* **207** : 270–272.

—— 1966. The Silurian brachiopod *Eocoelia hemisphaerica* (J. de C. Sowerby) and related species. *Palaeontology*, London, **9** : 523–543, pl. 83, 84.

——, Cocks, L. R. M. & Bambach, R. K. 1968. The Composition and Structure of Lower Silurian Marine Communities. *Lethaia*, Oslo, **1**: 1–27.